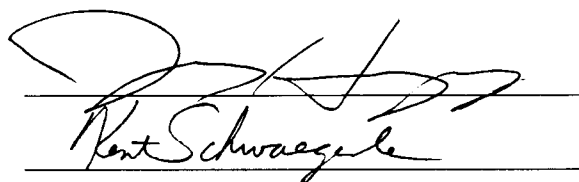


EFFECTS OF MIGRATORY GEESE ON PLANT COMMUNITIES AND NITROGEN
DYNAMICS IN AN ALASKAN SALT MARSH

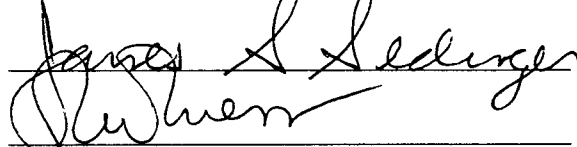
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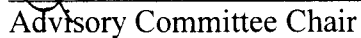
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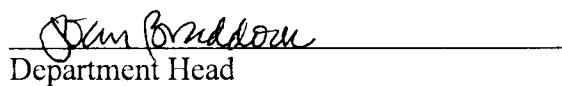
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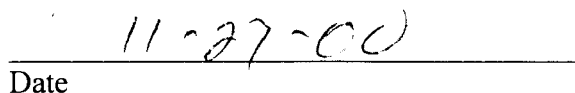

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EFFECTS OF MIGRATORY GEESE ON PLANT COMMUNITIES AND NITROGEN
DYNAMICS IN AN ALASKAN SALT MARSH

A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

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ABSTRACT

Herbivory is an integral component of ecosystems that impacts plant communities and ecosystem processes, and affects forage availability and quality for the herbivore. I investigated the effects of lesser snow geese (*Anser caerulescens caerulescens*) and Canada geese (*Branta canadensis*) on two salt marsh plant communities, a sedge meadow and an herb meadow, in Cook Inlet, Alaska. Geese used the marshes during spring migration for a brief period, and foraging intensity was low compared to other goose-grazing systems. Seventy percent of the snow goose diet was on belowground plant tissues, whereas 92% of the Canada goose diet was on aboveground shoots.

In the sedge meadow, where feeding was primarily on aboveground shoots, there was no effect of grazing on biomass of the dominant species *Carex ramenskii* and *Triglochin maritimum*, or on shoot nitrogen concentrations in these species (an index of forage quality). An experiment with captive geese found no effect of herbivory on biomass or nitrogen concentrations at foraging intensity ten times greater than that imposed by wild geese, indicating that this community is highly resilient to herbivory.

In the herb meadow, where snow geese fed on belowground tissues, biomass of *Plantago maritima* and *Potentilla egedii* was lower, and biomass of *Carex ramenskii* higher, on grazed compared to ungrazed plots. Plant species' response to herbivory was determined by plant growth form, the type of herbivory (above- or belowground), and competitive interactions. Light herbivore pressure in this community altered the relative abundance of forage species for geese.

In the sedge meadow community, geese increased nitrogen mineralization rates by trampling litter into wet soils. Litter incorporated into soils increased organic nitrogen pool size, decreased soil C:N ratios, and facilitated the growth of nitrogen-fixing cyanobacteria, all of which led to increased mineralization rates in grazed areas. Fecal nitrogen inputs were small and did not affect nitrogen availability. A captive goose experiment found that fecal additions ten-fold larger also had no effect on nitrogen availability. In the herb meadow, geese did not affect nitrogen mineralization because soils were dry with little standing water, so that incorporation of litter into soils through trampling was less important.

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PREFACE

The three chapters in this thesis were written and formatted for separate journals. Chapter 1 was in press at *Journal of Ecology* at the time the thesis was completed, chapter 2 was submitted to *Ecology*, and chapter 3 was submitted to the *Journal of Ecology*. As first author on these manuscripts, I did the writing and data analysis, and was responsible for the majority of the field and lab work. However, my co-authors on these manuscripts, Jerry Hupp at the U.S. Geological Survey, Biological Resources Division (USGS, BRD), and Roger Ruess at the Institute of Arctic Biology, University of Alaska Fairbanks (UAF), provided valuable assistance with ideas and with editing of manuscripts. In addition, Jerry spent countless hours in the field familiarizing me with the study area, helping to develop study design, collecting data, and, in general, training a novice biologist. Jerry also collected the data on goose esophageal contents in chapter 1. The use of the word “we” in the manuscripts reflects the substantial input provided by both my co-authors. However, I alone take responsibility for any errors in the work.

The work involved in this thesis could not have been completed without the generous financial support provided by the USGS, BRD. Other support was provided by an Angus Gavin Memorial Bird Research Grant, a UAF Office of Global Change Research Grant, and grants from the Arctic Institute of North America and the John Marr Ecology Fund. The graduate school at UAF provided stipends, tuition waivers, and a travel grant, and several scholarships from UAF filled in the financial gaps.

Many technicians and volunteers put in long days in the field under less than ideal conditions collecting data, setting up exclosures, and slogging through mud. Needless to

say, this project was only possible through the assistance of Allison Banks, Monette Boswell, Tim Bowman, Phil Busteed, Kelly Chapin, Jennifer Farnam, Cindy Hinshaw, Steve Reidsma, Carrie Talus, and Gail Volt. In particular, Lem Butler, who survived two field seasons and two winters in the lab, was instrumental in developing lab and field protocols, and was a great sounding board for ideas.

Many graduate students provided friendship, support, and ideas throughout my years at UAF, particularly Brian Person, Kate Doran, and Beth Lenart. I would also like to thank my committee members Kent Schwaegerle, Jim Sedinger, John Bryant, and Rich Boone for their ideas and their editing skills. Dana Thomas, Ron Barry, and Kent Schwaegerle assisted with statistics, and Lola Oliver and Allen Doyle with laboratory techniques. The Alaska Department of Fish and Game supported my work on a State Game Refuge, and provided the invaluable use of a truck on the west side of Cool Inlet. Jim Clinton, and Buck and Charlene Stewart kindly lent the use of their cabins in Susitna Flats. Bob Freeman and others in Beluga provided logistic support and friendship while we were in the field.

The support of my family has been crucial to the completion of this project. Thanks to my husband Matt Sweetsir and our daughter Hayley for hanging in there when I missed summer outings, Saturdays at the pool, and dinners together because I was writing. Other family members, particularly my sister-in-law Kiki Stirling and my parents, Carl and Barbara Zacheis, provided wonderful support by pitching in on babysitting and doing little extras like making Halloween costumes and providing stress-free vacations. Finally, with incredible gratitude I thank my mother-in-law, Pat Hill, who

has provided a warm, loving, stimulating environment for Hayley to grow up in for the many, many days I've had to be away at school.

INTRODUCTION

Herbivory is an integral component of ecosystems that affects plant communities and ecosystem processes. Herbivory by geese may affect the productivity (Cargill & Jefferies 1984; Giroux & Bédard 1987a; Hik & Jefferies 1990; Bélanger & Bédard 1994; Gauthier *et al.* 1995), above- or belowground biomass (Smith & Odum 1981; Bélanger *et al.* 1990; Esselink *et al.* 1997; Hupp *et al.* 2000), species composition (Bazely & Jefferies 1986), or relative species abundance (Smith 1983; Bazely & Jefferies 1986; Giroux & Bédard 1987a) of a plant community. The specific effects of geese on plant communities depend on many factors, such as the frequency and duration of herbivory (Hik & Jefferies 1990; Hik *et al.* 1991), the amount of biomass removed (Giroux & Bédard 1987b), and the type of herbivory (i.e., on above- or belowground plant tissues). Plant characteristics, such as growth form (Hyder 1972; Archer & Tieszen 1986; Rosenthal & Kotanen 1994) and the phenological stage of the plants (Hik & Jefferies 1990; Hik *et al.* 1991) also influence community and individual plant response to herbivory. In addition, the composition of the plant community may in turn determine the effects of herbivory on individual species (Crawley 1990).

Herbivory also affects ecosystem processes, particularly cycling of nitrogen. Herbivory may increase or decrease the rate at which nitrogen becomes available to plants, primarily by altering litter or root biomass (Holland & Detling 1990; Pastor *et al.* 1993; Biondini *et al.* 1998; van Wijnen *et al.* 1999), altering the decomposability of litter (Pastor *et al.* 1993; Ritchie *et al.* 1998; Sirotiak & Huntly 2000), and through the addition of waste products (Bazely & Jefferies 1985; Ruess & McNaughton 1987;

Thomas *et al.* 1988; Day & Detling 1990; Pastor *et al.* 1993; Zaady *et al.* 1996). The specific effects of herbivory on nitrogen cycling again depend on many factors, such as plant community composition (Sirotnak & Huntly 2000), the quantity of fecal input (Frank *et al.* 1994; Frank & Groffman 1998), the extent and type of vegetative cover (Gauthier *et al.* 1995; Beaulieu *et al.* 1996), soil moisture (Zaady *et al.* 1996), and soil organic matter content (Manley *et al.* 1995).

The effects of herbivory on community and ecosystem processes may result in altered forage quality or quantity for the herbivore, with effects ranging from negative to positive. The nitrogen concentration of vegetation, an important determinant of forage quality, is often increased or maintained longer in the growing season by grazing and/or by the addition of excreta (Ydenberg & Prins 1981; Bazely & Jefferies 1985; Day & Detling 1990; Hik & Jefferies 1990; Thomas *et al.* 1990; Gauthier *et al.* 1995). Moderate intensity grazing may increase the productivity of forage species (McNaughton 1979; Cargill & Jefferies 1984; Hik & Jefferies 1990), although this effect may not appear without the addition of fecal nitrogen (Hik & Jefferies 1990). Alternatively, herbivory may reduce or not affect the availability of forage (Smith & Odum 1981; Giroux & Bédard 1987a; Zellmer *et al.* 1993; Gauthier *et al.* 1995; Bakker & Loonen 1998; Person *et al.* 1998), or have no effect on forage quality (Bélanger *et al.* 1990; Zellmer *et al.* 1993).

I studied the effects of herbivory by lesser snow geese (*Anser caerulescens caerulescens*) and Canada geese (*Branta canadensis*) on plant communities and nitrogen cycling in Susitna Flats, a salt marsh in Cook Inlet, Alaska. Characteristics of this system

make it unusual compared to most systems where goose herbivory has been studied. Geese feed in the marsh for a short period in the early spring during migration to nesting areas in western Alaska and Russia, and most do not return during fall migration. Foraging intensity is low compared to other goose migratory, wintering, and nesting areas, as the duration of use by the geese is very short. Because it is early in the growing season when geese are in the marsh, there is little aboveground shoot growth. Snow geese grub for belowground plant tissues, whereas Canada geese graze on aboveground shoots. Therefore, plants may experience above- and/or belowground herbivory, but there is essentially one bout of feeding, and it is when plants are at an early developmental stage. This is in contrast to other goose-grazing systems, where areas may be re-grazed several times during the growing season (Prins *et al.* 1980; Gauthier *et al.* 1995; Person *et al.* 1998), and to staging and wintering areas, where forage biomass is much higher and duration of use is longer (Giroux & Bédard 1987a; Esselink *et al.* 1997). Soils at my study site had low organic matter and high moisture content, and, with little aboveground live plant material, were essentially bare in the spring when geese were in the marsh, except for a thin litter layer. These soil characteristics allowed goose activity to more easily impact soil processes.

I conducted this study in two separate plant communities within Susitna Flats, a sedge meadow and an herb meadow. One set of objectives was to determine which forage species and plant tissues geese fed on in order to identify which components of plant communities were exploited. A study using paired grazed/excused plots was designed to determine plant community response to herbivory, whether it differed

between the two communities, and whether herbivory affected forage availability to geese. The objectives of a second study were to determine if geese affected nitrogen availability to plants, under what conditions, and by what mechanism. I also wanted to determine whether altered nitrogen availability resulted in changes in plant tissue nitrogen concentrations, thus affecting diet quality for geese. To examine the effects of herbivory under more controlled conditions within the sedge meadow I set up an experiment using captive adult lesser snow geese. This experiment was designed to determine if high intensity feeding by geese would degrade plant communities, and if fecal nitrogen input affected plant response to herbivory.

EFFECTS OF MIGRATORY GEESE ON PLANT COMMUNITIES OF AN ALSAKAN SALT MARSH¹

Summary

1 We studied the effects of lesser snow geese (*Anser caerulescens caerulescens*) and Canada geese (*Branta canadensis*) on two salt marsh plant communities in Cook Inlet, Alaska, a stopover area used during spring migration. From 1995-97 we compared plant species composition and biomass on plots where geese were excluded from feeding to paired plots where foraging could occur.

2 Foraging intensity was low (650-1930 goose-days km⁻²) compared to other goose-grazing systems.

3 Canada geese fed mainly on above-ground shoots of *Triglochin maritimum*, *Puccinellia* spp., and *Carex ramenskii*, whereas the majority of the snow goose diet consisted of below-ground tissues of *Plantago maritima* and *Triglochin maritimum*.

4 Plant communities responded differently to goose herbivory. In the sedge meadow community, where feeding was primarily on above-ground shoots, there was no effect of grazing on the dominant species *Carex ramenskii* and *Triglochin maritimum*. In the herb meadow community, where snow geese fed on *Plantago maritima* roots and other below-ground tissues, there was a difference in the relative abundance of plant species between

¹In press at *Journal of Ecology* as Zacheis, A.B., Hupp, J.W., and Ruess, R.W. Effects of migratory geese on plant communities of an Alaskan salt marsh.

treatments. Biomass of *Plantago maritima* and *Potentilla egedii* was lower on grazed plots compared to exclosed, whereas biomass of *Carex ramenskii* was greater on grazed plots. There was no effect of herbivory on total standing crop biomass in either community. The variable effect of herbivory on *Carex ramenskii* between communities suggests that plant neighbours and competitive interactions are important factors in a species' response to herbivory. In addition, the type of herbivory (above- or below-ground) was important in determining plant community response to herbivory.

5 Litter accumulation was reduced in grazed areas as compared to exclosed in both communities. Trampling of the previous year's litter into the soil surface by geese incorporated more litter into soils in grazed areas.

6 This study illustrates that even light herbivore pressure can alter plant communities and affect forage availability.

Keywords: Canada goose, *Carex ramenskii*, herbivory, *Plantago maritima*, *Potentilla egedii*, snow goose, *Triglochin maritimum*

Introduction

Goose herbivory can significantly impact production, composition and species abundance of plant communities, and this may in turn affect forage availability. The effects of geese on plant communities are variable, and depend on factors such as foraging intensity, plant community composition, whether geese feed on above- or below-ground plant tissues and the ability of plant species to re-grow following damage. For example, goose grazing on above-ground plant material may increase (Cargill &

Jefferies 1984), decrease (Gauthier *et al.* 1995), or have no effect (Person *et al.* 1998) on the primary productivity of a plant community, whereas grubbing for below-ground tissues usually decreases productivity or the spatial extent of vegetation (Smith & Odum 1981; Kerbes *et al.* 1990; Bélanger & Bédard 1994; Ganter *et al.* 1996; Miller *et al.* 1996; Esselink *et al.* 1997; Jano *et al.* 1998). Within an ecosystem, individual plant species may show different re-growth patterns and productivity under similar grazing intensities (Kotanen & Jefferies 1987; Bazely & Jefferies 1989; Hik & Jefferies 1990; Zellmer *et al.* 1993; Gauthier *et al.* 1995). In addition, the timing, intensity and frequency of defoliation, as well as the fertilising effect of faeces, alters the re-growth potential of some species (Prins *et al.* 1980; Hik & Jefferies 1990; Hik *et al.* 1991), while having no effect on others (Beaulieu *et al.* 1996). Finally, the response of a plant species to herbivory may vary depending on the plant community in which it is growing, and who its neighbours are (Crawley 1990).

Increasing populations of some goose species, including the North American mid-continent population of lesser snow geese (*Anser caerulescens caerulescens* L.), have raised interest in the effects of geese on their environment (Abraham & Jefferies 1997; Ankney 1996). By grubbing for below-ground plant tissues, snow geese can degrade habitat in wintering and nesting areas, and along migratory routes (Jefferies 1988; Kerbes *et al.* 1990; Ganter *et al.* 1996; Miller *et al.* 1996; Srivastava & Jefferies 1996; Jano *et al.* 1998). The degradation of Arctic and subarctic wetlands are of particular concern as are the effects of this loss of habitat on snow goose and other waterbird populations (Cooch & Cooke 1991; Williams *et al.* 1993; Ankney 1996; Ben-Ari 1998). Studies of the

impacts of geese on their environment have focused on areas where herbivory is intense, and where the effects of geese on plant communities are visible, and sometimes destructive (*e.g.*, Giroux & Bédard 1987; Miller *et al.* 1996; Srivastava & Jefferies 1996; Esselink *et al.* 1997; Person *et al.* 1998). Less research has been conducted in systems with less intense herbivore pressure, although such cases can provide information on threshold levels of herbivory that plant communities can sustain before the habitat is degraded (Archer & Smeins 1991).

We examined the effects of snow and Canada goose (*Branta canadensis* L.) activity on two plant communities in a salt marsh in south-central Alaska used during spring migration. Geese used the area only during a brief period each spring, and did not return to feed until the following spring. Thus, our study provides information on the response of a subarctic salt marsh to relatively light intensities of goose foraging. Also, because Canada geese and snow geese simultaneously used the same habitats, our study provides information on whether forage removal affected subsequent forage abundance for one or both species. Our objectives were (i) to determine which plants were used as foods by Canada and snow geese and thus whether diet differed between species; (ii) to estimate feeding intensity and forage removal within the marsh; and (iii) to determine if plant response to goose herbivory varied between two major plant communities.

Study Area

This study was conducted in a 20.82 km² portion of Susitna Flats, a 100 km² salt marsh located in Upper Cook Inlet, Alaska (61°15' N, 150°30' W) (Fig. 1). Elevation of

this coastal wetland gradually increases by 1 m from the shore to the beginning of woody vegetation, a distance of 1.5 to 3 km (A. Zacheis, unpublished data). Plant communities show a pronounced zonation parallel to the shore (Vince & Snow 1984). Geese use Susitna Flats in April and early May and at this time there is little above-ground vegetation, except for overwintering shoots of *Carex* spp. and small amounts of new shoot growth.

Up to 34,000 lesser snow geese use Cook Inlet salt marshes during spring migration to nesting areas on Wrangel Island, Russia (Butler & Gill 1987). The Wrangel Island snow goose population is less than 50% of its historic level and unlike other snow goose populations has not increased in recent years (Kerbes *et al.* 1999). Snow geese arrived in our study area in mid-April. Their numbers peaked in late April, and they departed during the first week of May, so that residence time was 10-20 days. We estimated goose use of the study area from aerial and ground surveys done in 1993–97 (J. Hupp, W. Eldridge, unpublished data). Estimates of goose-days km^{-2} were made by summing the number of geese observed each day, and correcting this by a sampling fraction (number of days of observation/total number of days geese were in Susitna Flats) (Giroux & Bédard 1988). This was divided by the area of the study site to give estimates of 450-1300 goose-days km^{-2} for 1993-96. Counts done in 1997, which were limited to a brief period in April when snow geese were present, indicated that snow goose numbers were much lower than in previous years (30 goose-days km^{-2}) (J. Hupp, unpublished data).

Up to 100,000 Canada geese also use Upper Cook Inlet as spring migration

habitat (Butler & Gill 1987). Most are Taverner's (*B. c. taverneri* Delacour) and cackling Canada geese (*B. c. minima* Ridgway) that nest in western Alaska (King & Derksen 1986). Reliable population estimates for Taverner's Canada geese are not available; however, the population of cackling Canada geese has increased approximately 12% annually since 1988 (Wilkins & Cooch 1999). During 1995-97 Canada goose use of the study area was between 480 and 830 goose-days km⁻² (J. Hupp, W. Eldridge, unpublished data). Canada geese tend to arrive earlier and stay later than snow geese so that residence times were between four and seven days longer.

Virtually all goose feeding in our study area occurred in early spring. Snow geese do not nest in Cook Inlet and rarely use the area during the autumn migration. Although small numbers of Canada geese nest in Cook Inlet, we observed no nesting pairs or broods on our study area. Some Canada geese do use Cook Inlet wetlands as staging areas in autumn but numbers are smaller than in spring and most flocks remain along the outer coastal fringe of wetlands. We observed no evidence of autumn feeding on our plots.

We conducted our research in two plant communities (Fig. 1) used by geese (properties described in Table 1). The sedge meadow community was composed mainly of *Carex ramenskii* Kom. and *Triglochin maritimum* L. (nomenclature follows Hultén 1968). The herb meadow community was dominated by *Triglochin maritimum*, *Potentilla egedii* Wormsk., *Plantago maritima* L., and *Carex ramenskii*. Soil moisture, soil salinity, and frequency of tidal flooding were all higher in the sedge meadow community.

Methods

GOOSE DIETS

From 18-28 April in each of three years (1996-98), we used a rifle or shotgun to collect snow geese and Canada geese from flocks that we observed feeding in coastal wetlands throughout Upper Cook Inlet. Geese were collected under permits authorised by the U.S. Fish and Wildlife Service (permit number PRT-789758) and the Alaska Department of Fish and Game (permit numbers 96-51, 97-021, and 98-031). Habitats where geese were collected were similar to those where we studied the effects of goose foraging. Oesophageal contents were removed following collection, washed in fresh water in a fine-mesh sieve, and frozen. We later thawed samples and separated material by species and plant part (above-ground vs. below-ground tissue). We identified forage items by comparison to reference material. Although freezing of samples softened oesophageal contents, individual forage items were clearly recognisable. Samples were dried to constant mass at 60 °C and weighed (± 0.01 g). We calculated aggregate percent dry mass of each item in the diet as the average of the proportions of each food item within each bird (Swanson *et al.* 1974). Analysis was based only on individuals that had > 0.05 g (dry mass) of forage in their oesophagi. Geese collected at the same time and location usually fed on similar items. Therefore, we pooled data (within goose species) from birds that were collected at the same time and location before we calculated aggregate percent dry mass.

EFFECTS OF GEESE ON PLANT COMMUNITIES

To examine the effects of herbivory on plant species composition and litter accumulation, we set up paired grazed/exclosed plots in the two plant communities. Eight pairs of plots were located at approximately 15 m intervals along 115 m long transects. Plots were 1 m². Members of a pair were usually separated by 5 m and were in similar vegetation, based on visual cover estimates. One plot of each pair was randomly selected to receive an exclosure treatment. We established two transects in the sedge meadow community and nine transects in the herb meadow community (Fig. 1). Transects were separated by a minimum of 200 m.

We established plots in August of 1994. In early April of 1995, 1996, and 1997, before snow had melted, we erected 0.5 m tall fences around exclosed plots, and left the other plots open to goose foraging. Fences contained the 1 m² plot and a border of at least 25 cm. Exclosures were constructed of 2 cm mesh herring seine stretched around reinforcement rod at the corners, except in 1995 when we encircled plots with three levels of twine wrapped around corner posts. Use of the herring seine allowed the sides of the exclosure to fall to the ground as the snow melted. Twine was crossed over the tops of exclosures in all years. Exclosures were taken down in late May, after geese had left the study area.

We clipped sub-samples of above-ground vegetation from each plot each year in August from 1994 through 1997. The sample in 1994 was to determine if there were pre-treatment differences between paired plots. In 1994 and 1995, all above-ground biomass

in one randomly selected 25 cm x 25 cm quadrat in each plot was clipped. In 1996 and 1997, two randomly selected, smaller quadrats (25 cm x 12.5 cm) were clipped in each plot. We clipped two quadrats in 1996 and 1997 to incorporate more of the spatial variation in plant cover within plots into our sample. Clipped quadrats and areas directly adjacent to them were not sampled in subsequent years. In all years, clippings were washed in fresh water, standing dead material was separated from live, and live biomass was sorted by species. *Puccinellia* species were combined, because *Puccinellia phryganodes* (Trin.) Scribn. & Merr. and *Puccinellia nutkaensis* (Presl) Fern. & Weath. may be ecophenes (Snow 1982). Total above-ground live biomass was the sum of the biomass of all species. In 1996 and 1997, litter lying on the soil surface was collected from quadrats where vegetation was clipped. All samples were frozen for transport to the University of Alaska, where they were dried at 60 °C to constant mass and weighed (\pm 0.01 g).

Beginning in 1995, we counted the number of inflorescences or flowers for the dominant species (*Triglochin*, *C. ramenskii*, *Potentilla*, and *Plantago*) from the sampled quadrats, except that *C. ramenskii* inflorescences were not counted until 1996. In 1996 and 1997, we counted plant densities of the dominant species within two 9 cm x 12.5 cm quadrats within each plot. For *Triglochin*, *C. ramenskii*, and *Plantago*, we counted where plant bases emerged from the soil (basal meristem locations), and for *Potentilla*, we counted the locations where petioles and roots grew from stolons. Estimates of total plant and inflorescence densities did not include *Puccinellia* or other species that were relatively rare on plots.

In August 1997 we sampled below-ground biomass by taking one soil core (5.5 cm diameter by 10 cm deep) in each of the 25 cm x 12.5 cm quadrats where above-ground biomass had been harvested that year. Collections were made from plots along three transects in the herb meadow community, and from all plots in the sedge meadow community. Soil cores were stored in polyethylene bags, frozen within three days, and transported to the University of Alaska, where roots and rhizomes were washed free of soil, dried at 60 °C to constant mass, and weighed (± 0.01 g). No attempt was made to separate dead from live biomass or to separate biomass by species.

FORAGING INTENSITY

Offtake plots

To estimate the amount of vegetation removed by geese (offtake), we established a series of small (25 cm x 25 cm) paired grazed/exclosed offtake plots in April of 1996 and 1997. Four pairs of offtake plots were located near each transect of 1 m² plots, generally within 0.5 m to 2 m of alternating grazed plots along the transect. Paired offtake plots were separated by 0.5 m to 1 m. Offtake plots were set up at different locations along transects in each of the two years. In 1996 offtake exclosures were cylinders of chicken wire anchored with reinforcement rod, whereas in 1997 we used herring seine to surround offtake plots.

Offtake plots were sampled as soon as possible in May, usually one to three weeks after geese had fed on them. We removed all soil and vegetation in the offtake plots to a depth of approximately 10 cm, and washed most of the soil from the vegetation

in the field. Vegetation was re-washed in the field laboratory, and shoot material sorted to species. *Plantago* roots and *C. ramenskii* rhizomes were also sampled. Samples were immediately frozen, and later dried at 60 °C to constant mass before weighing (± 0.001 g).

Faecal counts

We also attempted to estimate foraging intensity by counting goose faeces on the grazed 1 m² transect plots. In 1995 and 1996, high tides and goose trampling of wet faeces made accurate counts impossible. However, 1997 was a dry spring with early snowmelt, and we were able to count faeces on plots reliably. We counted faeces along each transect once, as soon as we could access plots after birds left an area. We could easily differentiate between fresh faeces and those from previous years, as year-old faeces were considerably decayed and desiccated.

STATISTICAL ANALYSIS

We analysed the pre-treatment (1994) biomass data as a doubly blocked ANOVA, with pairs of plots (inner blocks) nested within transects (outer blocks). Plant communities and each major species within a community were analysed separately. This ANOVA model is equivalent to a paired t-test (Sokal & Rohlf 1995), but is preferable to a t-test, as it incorporates an additional level of blocking (transects). We tested for treatment effect (exclosure, no exclosure) with the residual mean square as the error term (Newman *et al.* 1997). We used the same ANOVA model to analyse offtake data, with

the data separated by year, plant community and species.

Biomass data from 1995 through 1997 were analysed as repeated measures MANOVAs, with the same doubly blocked design. We used an autocorrelation function analysis to confirm that plots pairs (inner blocks) were independent and could be considered replicates on which the repeated measures were made. Plant communities were again analysed separately; individual species biomass and total biomass were analysed in separate repeated measures. The sum of the two 25 cm x 12.5 cm quadrats sampled within each plot in 1996 and 1997 was used in the repeated measures, so that the data structure was comparable to that in 1995. The same repeated measures MANOVA model was used to analyse litter biomass, standing dead material, species richness and inflorescence and plant densities. In cases where a year x treatment effect was significant, but an overall treatment effect was not, years were analysed separately using the univariate ANOVA model.

All data were transformed (either \log_e+1 or square root+3/8) to correct for non-normality and non-constancy of error variance (Neter *et al.* 1990; Zar 1996). However, most analyses were also run on ranked data, as transformations did not guarantee that the assumptions of ANOVA were met (Conover 1980; Johnson & Wichern 1992). We report the results of the analyses using transformed data, as in most cases results on the ranked data were similar (Conover 1980). Exceptions are noted in the text. Non-transformed means ± 1 SE are reported throughout.

Results

GOOSE DIETS

We examined oesophageal contents of 45 snow geese and 28 Canada geese. Because we pooled data from individuals that were collected at the same time and location, analysis was based on 28 and 25 samples from snow geese and Canada geese, respectively.

Sixty-nine percent of the snow goose diet was below-ground forage whereas only 8% of the Canada goose diet consisted of below-ground plant parts (Fig. 2). Snow geese fed primarily on roots of *Plantago* that were 1-4 mm in diameter, and also on *Triglochin* root crowns. Snow geese also consumed above-ground shoots of *Triglochin*, *Carex lyngbyae* Hornem. and *C. ramenskii*, including basal meristematic tissue. They rarely ate green tips of vegetation. In contrast, Canada geese grazed primarily on green tips of *Puccinellia*, *Triglochin*, and *C. ramenskii* shoots. They did not usually consume the meristem at the base of shoots. Most birds (61% and 56% of snow geese and Canada geese, respectively) had consumed more than one forage species.

FORAGING INTENSITY

Offtake plots

In the sedge meadow community, there were no significant differences between grazed and exclosed offtake plots in 1996 or 1997 for either *C. ramenskii* biomass (1996: $F_{1,5} = 0.0002$, $P = 0.99$; 1997: $F_{1,7} = 0.29$, $P = 0.61$), *Triglochin* biomass (1996: $F_{1,5} =$

0.05, $P = 0.83$; 1997: $F_{1,7} = 1.47$, $P = 0.27$), or total biomass (1996: $F_{1,5} = 0.03$, $P = 0.87$; 1997: $F_{1,7} = 0.44$, $P = 0.53$).

In the herb meadow community in 1996 there was 25% less *Plantago* shoot biomass in grazed offtake plots ($0.98 \pm 0.24 \text{ g m}^{-2}$) than in exclosures ($1.32 \pm 0.27 \text{ g m}^{-2}$; $F_{1,33} = 3.98$, $P = 0.05$). *Plantago* roots showed a similar (26%) reduction in biomass in grazed plots ($28.24 \pm 7.93 \text{ g m}^{-2}$) compared to exclosures ($38.18 \pm 8.24 \text{ g m}^{-2}$), although in this case it was not statistically significant ($F_{1,33} = 2.75$, $P = 0.11$). We included all *Plantago* roots in our offtake samples, although snow geese fed on only smaller diameter roots and not on thicker taproots. The large biomass of the taproots may have swamped any statistically significant removal of smaller roots. *Potentilla* showed the greatest response to use by geese, with 45% less biomass in grazed offtake plots ($0.08 \pm 0.02 \text{ g m}^{-2}$) compared to exclosed ($0.14 \pm 0.03 \text{ g m}^{-2}$; $F_{1,33} = 9.10$, $P = 0.005$). There were no differences in biomass of *Triglochin* ($F_{1,33} = 0.60$, $P = 0.44$), *Puccinellia* ($F_{1,33} = 0.57$, $P = 0.45$), or *C. ramenskii* ($F_{1,33} = 0.05$, $P = 0.83$) between exclosed and grazed offtake plots in 1996. The 18% reduction in total biomass in grazed offtake plots ($49.96 \pm 7.46 \text{ g m}^{-2}$) compared to exclosed ($60.70 \pm 7.97 \text{ g m}^{-2}$) was not statistically significant ($F_{1,33} = 2.82$, $P = 0.10$).

In the herb meadow community in 1997, a year of lower foraging intensity, there were no significant differences between exclosed and grazed offtake plots for any of the dominant species, or for total biomass (*Triglochin*: $F_{1,35} = 0.01$, $P = 0.93$; *Plantago* shoots: $F_{1,35} = 0.72$, $P = 0.40$; *Plantago* roots: $F_{1,35} = 0.07$, $P = 0.79$; *Potentilla*: $F_{1,35} =$

1.00, $P = 0.32$; *Puccinellia*: $F_{1,35} = 1.26$, $P = 0.27$; *C. ramenskii*: $F_{1,34} = 0.11$, $P = 0.74$; total biomass: $F_{1,35} = 0.001$, $P = 0.98$).

Faecal counts

Faecal counts in 1997 indicated slightly greater use by geese of the sedge meadow community (1.8 ± 0.4 faeces m^{-2}) than the herb meadow community (1.3 ± 0.2 faeces m^{-2}).

EFFECTS OF GEESE ON PLANT COMMUNITIES

Sedge meadow community

There were no pre-treatment differences in the biomass of the dominant species within the sedge meadow community between designated grazed and exclosed plots in 1994 (*C. ramenskii*: $F_{1,15} = 2.82$, $P = 0.11$; *Triglochin*: $F_{1,15} = 0.30$, $P = 0.59$).

Exclosures had little effect in the sedge meadow community. There was no difference in the biomass of the dominant species *C. ramenskii* and *Triglochin* between exclosed and grazed plots, and no difference in total live biomass for any of the three years of treatment (Fig. 3a-c, Table 2). In addition, there was no effect of exclosures on the density of either dominant species, or on total plant density (Fig. 4a-c, Table 2). *C. ramenskii* had more inflorescences in grazed plots (Fig. 4d, Table 2). This resulted in more total inflorescences in grazed areas, despite a lack of exclosure effects on *Triglochin* (Fig. 4e,f, Table 2). There was no difference in root biomass between

exclosed ($212.41 \pm 15.56 \text{ g m}^{-2}$) and grazed ($236.19 \pm 12.48 \text{ g m}^{-2}$) plots in 1997 after three years of fencing ($F_{1,31} = 2.08$, $P = 0.16$).

Litter accumulation was greater within exclosures, although there was no effect of exclosures on standing dead material (Fig. 3d,e, Table 2). There was no treatment effect on species richness per 25 cm x 25 cm quadrat for all years ($F_{1,15} = 0.03$, $P = 0.86$). Mean species richness for the three years of the study was 2.1 ± 0.1 in grazed plots and 2.2 ± 0.1 in exclosed plots.

Herb meadow community

In the herb meadow community there were no pre-treatment differences in the biomass of any dominant species between designated exclosed and grazed plots in 1994 (*Triglochin*: $F_{1,71} = 1.10$, $P = 0.30$; *Plantago*: $F_{1,71} = 0.0002$, $P = 0.99$; *Potentilla*: $F_{1,71} = 3.21$, $P = 0.08$; *Puccinellia*: $F_{1,71} = 0.13$, $P = 0.72$; *C. ramenskii*: $F_{1,71} = 2.73$, $P = 0.10$).

Plant species responded differently to fencing. There were no treatment effects on biomass, plant density, or inflorescence density for *Triglochin* (Figs. 5a and 6a,f, Table 2). In contrast, *Plantago* had less biomass and lower plant densities in grazed plots (Figs. 5b and 6b, Table 2). *Plantago* inflorescence density had a significant year*treatment interaction, with lower densities in grazed plots not evident until the third year of fencing (univariate ANOVAs: 1995: $F_{1,71} = 2.29$, $P = 0.13$; 1996: $F_{1,143} = 1.18$, $P = 0.28$; 1997: $F_{1,143} = 10.56$, $P = 0.001$) (Fig. 6g, Table 2). *Puccinellia* also had less biomass in grazed plots (Fig. 5d, Table 2).

Potentilla had greater biomass, plant density and flowering within exclosures (Figs. 5c and 6c,h, Table 2), representing the greatest response to grazing among species. There was a year x treatment interaction for biomass and inflorescence density (Table 2), due to annual variability in the difference between exclosed and grazed plots (Figs. 5c and 6h).

C. ramenskii was the only species with greater biomass, plant density and inflorescence density in grazed plots (Figs. 5e and 6d,i, Table 2). There was a steadily increasing difference in biomass between treatments (16% more biomass in grazed plots in 1995, 44% more in 1996, and 59% more in 1997), resulting in a weak year*treatment interaction, significant on the ranked data only ($F_{2, 70} = 3.15$, $P = 0.05$; compare with Table 2). Similarly, treatment differences in plant and inflorescence densities increased between 1996 and 1997 (Fig. 6d,i), resulting in a significant year*treatment interaction for inflorescences (Table 2). However, analysis on the ranked inflorescence data only showed a marginally significant year*treatment interaction ($F_{1, 71} = 3.18$, $P = 0.08$).

For each of the three years of exclusion of geese, total live biomass in the herb meadow community in August did not differ between treatments (Fig. 5f, Table 2), although there was a substantial shift in the proportion of *Plantago*, *Potentilla*, *Puccinellia* and *C. ramenskii* within the plant community (Fig. 5b-f). Total plant and inflorescence density also did not differ between exclosed and grazed plots (Fig. 6e,j, Table 2). Total inflorescence density had a year*treatment interaction because densities were slightly higher in exclosures in 1996, but higher in grazed areas in 1997 (Fig. 6j). There was no difference in root biomass between exclosed plots ($168.05 \pm 13.38 \text{ g m}^{-2}$)

and grazed plots ($173.40 \pm 13.15 \text{ g m}^{-2}$) upon completion of the study in 1997 ($F_{1,47} = 0.04$, $P = 0.85$).

We found more litter within exclosures compared to grazed plots in 1996 and 1997 (Fig. 5h, Table 2). There was also more standing dead material within exclosures, although treatment differences were not as pronounced as the litter effect (Fig. 5g, Table 2). There was a significant year*treatment interaction for standing dead due to annual variability in treatment differences (Fig. 5g).

We found no difference in species richness per 25 cm x 25 cm quadrat between exclosed and grazed plots for all years ($F_{1,71} = 1.17$, $P = 0.28$). Mean species richness for the three years of the study was 4.6 ± 0.1 in grazed plots and 4.8 ± 0.1 in exclosed plots.

Discussion

GOOSE DIETS

With the exception of *Potentilla*, geese consumed all major wetland plant species in the sedge meadow and herb meadow communities. The presence of more than one forage item in most oesophagi indicated that geese probably consumed whichever plants were present at feeding sites. *Potentilla* was probably not a forage item because it exists as a tiny corm in early spring and was a relatively minor part of the total biomass available to geese.

Although Canada geese and snow geese often exploited the same habitats and frequently fed in mixed flocks, there was little dietary overlap. *Plantago* roots were 40%

of the snow goose diet but only 2% of the Canada goose diet. *C. ramenskii* and *Triglochin* combined were 40% and 53% of snow goose and Canada goose diets, respectively. However, snow geese primarily exploited below-ground parts or non-photosynthetic basal portions of shoots, whereas Canada geese fed almost exclusively on above-ground green shoots of these species. Thus diets were largely partitioned by plant part. Prevett *et al.* (1985) also found that snow geese consumed more below-ground material than Canada geese did during spring staging at coastal habitats in James Bay, Canada.

FORAGING INTENSITY

Estimates of combined use by Canada and snow geese for our study area were 930, 1930, and 650 goose-days km⁻² for 1995, 1996, and 1997 respectively, several orders of magnitude less than estimates in other goose staging areas. Use of the 1.47 km² Montmagny sanctuary along the St. Lawrence River, a spring and fall staging area for greater snow geese (*Anser caerulescens atlantica*), was 34 000 goose-days km⁻² in the spring and 197 300 goose-days km⁻² in the fall (Bélanger *et al.* 1990). The 7.6 km² Dutch portion of the Ems Dollard estuary, bordering the North Sea, is used by greylag geese (*Anser anser*) as a spring and fall staging area, with some geese remaining throughout the winter (Esselink *et al.* 1997). Estimated goose use ranged from 32 900 to 80 300 goose-days km⁻² for 1983 to 1994 (Esselink *et al.* 1997). Lesser snow geese use wetlands along the coast of Hudson Bay for staging, nesting, and brood-rearing, where they grub for roots and rhizomes in the spring, and graze above-ground vegetation in the summer

(Jefferies 1988; Kerbes *et al.* 1990). At the McConnell River colony on Hudson Bay the 1985 estimate of breeding pair density was 132 299 pairs in a 339.7 km² area (Kerbes *et al.* 1990). Assuming birds arrived by 1 June and departed by 15 August (exact dates were not published), this translates into 58 000 goose-days km⁻² (Kerbes *et al.* 1990). This is an underestimate of herbivore pressure, however, as it does not include use by goslings, non-breeders, and spring migrants. Foraging intensity is also very high at the La Pérouse Bay colony, with 1990 estimates of 22 500 nesting pairs of geese, their goslings, and additional geese stopping over during migration (Jefferies 1988; Cooke *et al.* 1995). Nest density can reach as high as 2000 nests km⁻² (Kotanen & Jefferies 1997).

Not only is herbivore pressure relatively light in Susitna Flats, but the return time of geese to a specific portion of the marsh is a minimum of one year, as annual distributions of geese may vary. Snow goose flocks tend to feed along, and follow, the edge of the melting snow pack, so that the distribution of available habitat may vary among years depending on patterns and timing of snowmelt (J. Hupp, unpublished data). For example, in 1997 snowmelt was unusually early, and snow goose use of the largely snow-free herb meadow community was light. However, the sedge meadow community, which became snow-free later, tended to have more use.

There were no significant differences in the biomass of *Triglochin*, *C. ramenskii* or *Puccinellia* between grazed and exclosed offtake plots in 1996 or 1997, although all were forage items found in the oesophagi of geese. In addition, we frequently found evidence of herbivory on these plants (*e.g.*, grazed shoot tips). These plant species may be quite tolerant to herbivory and may have replaced lost tissue between the incidence of

herbivory and the time we sampled plots one to three weeks later. Alternatively, the small size and limited number of offtake plots, and the variability in goose distribution, may have made it unlikely that all plots were fed on, or fed on to a sufficient extent that significant differences between grazed and exclosed plots could be detected.

There was 25% less *Plantago* root and shoot biomass in grazed offtake plots as compared to exclosed in 1996, although the difference in root biomass was not statistically significant. In 1997 there was 2% less *Plantago* root biomass in grazed plots, again not a significant difference. We may have been unable to detect significant reductions in biomass of below-ground forage due to high spatial variability in plant biomass and in snow goose feeding sites. Similarly, in the St. Lawrence staging area, Giroux and Bédard (1987) were unable to document differences in below-ground biomass before and after greater snow geese fed in area, due to high variability in biomass. However, the larger reduction in *Plantago* root biomass in 1996, when there was greater use of the herb meadow community by snow geese, compared to 1997, suggests that geese likely had an effect on the abundance of this forage species. The 45% reduction of *Potentilla* in grazed offtake plots in 1996 suggests that this species was also affected, although it is not a forage item.

EFFECTS OF GEESE ON PLANT COMMUNITIES

Sedge meadow community

The impact of geese varied between the two plant communities. In the sedge meadow community, feeding was primarily on above-ground shoots, although snow

geese may also have fed on *C. ramenskii* rhizomes and the upper portion of *Triglochin* rootstocks, and removed meristematic tissue in both species. Herbivory had no effect on total live biomass in August, or on the biomass of the dominant species *C. ramenskii* or *Triglochin*. The dominant species in this community have characteristics conferring tolerance to herbivory, such as below-ground carbohydrate reserves, multiple meristems and carbohydrate production in undamaged tillers or shoots (Youngner 1972; Archer & Tieszen 1986; Rosenthal & Kotanen 1994; Crawley 1997). *C. ramenskii* has been shown to tolerate clipping, so that productivity in repeatedly clipped plots is equal to or greater than that in unclipped plots (Ruess *et al.* 1997), and *Triglochin* has a large rootstock from which carbohydrate reserves may be mobilised. The stability of this plant community's response to herbivory is likely due to minimal amounts of below-ground feeding and tolerance of the dominant species to above-ground herbivory. In addition, herbivore pressure is light, and herbivore return time is a minimum of one growing season. In contrast, other staging and wintering areas used by snow geese have longer residence times, shorter return times, and greater amounts of below-ground grubbing, resulting in reduction of productivity, reduction in biomass of forage species, and, at extreme goose densities, destruction of wetland vegetation (Smith & Odum 1981; Giroux & Bédard 1987; Kerbes *et al.* 1990; Bélanger & Bédard 1994; Ganter *et al.* 1996; Miller *et al.* 1996; Srivastava & Jefferies 1996).

The sample size of 16 paired plots within the sedge meadow community allowed detection of only relatively large differences between treatments. In 1997 treatment differences in *C. ramenskii* biomass had to be greater than 30% of the average biomass

on plots to be statistically significant. Similarly, treatment differences in *Triglochin* biomass and total biomass had to be 36% and 21%, respectively, to be significant. However, mean differences between biomass on grazed and exclosed plots in 1997 were actually very small (6.5% more *C. ramenskii* biomass in exclosures, 3.7% less *Triglochin*, and 0.4% less total biomass). Therefore, we believe that our failure to detect a treatment effect is because herbivory did not substantially affect biomass within this community.

Herb meadow community

Herbivory significantly reduced the biomass of several plant species within the herb meadow community. *Plantago* was unable to compensate for root loss, and grubbing by snow geese resulted in lower biomass, plant density and inflorescence density in grazed plots. Dormann *et al.* (2000) similarly found *Plantago* biomass to be greatly reduced by brent geese (*Branta bernicla bernicla*) feeding on leaves and roots. Other saltmarsh perennials such as *Scirpus* spp. and *Spartina* spp. have also shown reductions in production, cover, or spatial extent due to feeding by geese on below-ground tissues (Smith & Odum 1981; Giroux & Bédard 1987; Esselink *et al.* 1997). *Potentilla* also appears unable to tolerate use by geese. Although it is not a forage species, grubbing for *Plantago* roots by snow geese may incidentally damage *Potentilla*. Because of its small size in the spring, *Potentilla* has little storage capacity or above-ground growth that would enable it to recover from tissue loss. *Potentilla* corms are shallowly rooted near the soil surface where disturbance may cause high rates of

mortality. This would explain the 45% reduction in *Potentilla* in grazed offtake plots as compared to exclosed plots, and the strong reductions in standing crop biomass, plant density, and flowering at the end of the growing season in grazed areas.

Competitive interactions, along with different tolerances to herbivory among plant species, are probably responsible for the shifts in relative species abundance within the herb meadow community. Whereas the decreased abundance of *Plantago* and *Potentilla* in grazed areas is likely to be due to the inability of these species to re-grow following below-ground herbivory or disturbance, greater growth of *C. ramenskii* in grazed areas may be due to reduced competition from *Plantago* and *Potentilla* (Crawley 1983), as well as tolerance of above-ground herbivory (Ruess *et al.* 1997). Although we do not have data on competitive interactions within this plant community, negative correlations between species may indicate competitive relationships. There was a significant negative correlation between *Plantago* and *C. ramenskii* biomass for all years of this study (Table 3), which persisted after the effects of herbivory had been removed (exclosed plots only in Table 3). We also found a negative association between *Potentilla* and *C. ramenskii*, although this correlation was not significant in exclosed plots only (Table 3).

Canada geese grazed above-ground shoots of *Puccinellia*, which had lower biomass in grazed compared to exclosed plots. In contrast, *Puccinellia phryganodes* grazed by snow geese at La Pérouse Bay tolerated grazing, and under some conditions exhibited greater biomass and/or production in grazed plots (Cargill & Jefferies 1984; Hik & Jefferies 1990; Hik *et al.* 1991). In particular, *P. phryganodes* showed increased production only when goose faeces were present (Hik & Jefferies 1990). The reduced

growth of *Puccinellia* in grazed plots in Susitna Flats may be due to herbivory combined with low faecal nitrogen return. Alternatively, the negative response of *Puccinellia* to grazing may be due, at least partially, to increased competition with *C. ramenskii*. *Puccinellia* and *C. ramenskii* biomass was negatively correlated, suggesting a competitive relationship (Table 3).

Shifts in community composition or relative species abundance under herbivory have often been hypothesised to be caused by alterations of the competitive hierarchy within the plant community (*e.g.*, Inouye *et al.* 1980; Crawley 1990; Furbish & Albano 1994). Shifts in species composition were documented on staging grounds of the St. Lawrence estuary (Giroux & Bédard 1987). Grubbing of *Scirpus americanus* reduced its abundance, whereas *Zizania aquatica*, whose seeds and stems are only eaten in the autumn, increased on grazed relative to exclosed plots (Giroux & Bédard 1987). *Spartina patens* and *Scirpus robustus* responded in opposite directions to grubbing by snow geese in a North Carolina wintering area (Smith 1983). At La Pérouse Bay, *Carex subspathacea* and dicotyledons increased in abundance within exclosures, at the expense of *Puccinellia phryganodes* (Bazely & Jefferies 1986).

Our results from two different communities suggest that the interaction of herbivory and competition can cause shifts in relative species abundance if grazing intolerant plants are present, but may have no effect on a community if they are not. The type of herbivory (*i.e.*, above- or below-ground) is important in determining a plant species' ability to tolerate herbivory or to re-grow following damage. In addition, the effect of herbivory on a particular plant species may depend on the community in which

it is found (*e.g.*, *C. ramenskii* increased in biomass and density in grazed plots in the herb meadow community but did not increase in the sedge meadow community). Therefore, the response of an individual species to herbivory is partly dependent on plant community composition.

EFFECTS OF GEESE ON LITTER ACCUMULATION

Although we did not measure litterfall directly, litter production was likely the same on grazed and exclosed plots in the sedge meadow community. This is because neither total standing crop biomass at the end of the growing season nor relative species abundance differed between treatments. In the herb meadow community, standing crop biomass did not differ between grazed and exclosed plots but relative species abundance did, making inferences about litter production more difficult. However, we suggest that litter production may have been slightly greater, and certainly not less, in grazed plots than in exclosed plots in this community. More *C. ramenskii* grows in grazed areas, and this species produces large amounts of litter compared to the other plant species.

Although litter production was the same or greater in grazed plots compared to exclosed, we found less litter on the soil surface in grazed plots. We attribute the disappearance of litter in grazed areas to trampling by geese. Trampling of previous years' litter into the soil surface means that more litter is incorporated into the soil in grazed areas and less accumulates on the soil surface. Trampling may also reduce litter loss through tidal export. Litter accumulation within exclosures commonly occurs in vertebrate grazing and browsing systems (*e.g.*, Fuller *et al.* 1985; Bazely & Jefferies

1986; McNaughton *et al.* 1988; Pastor *et al.* 1993; Biondini *et al.* 1998; Evers *et al.* 1998; van Wijnen *et al.* 1999), although in some cases litter accumulation is greater in grazed areas (Ford & Grace 1998). With high herbivore pressure, grazing or browsing tends to reduce above-ground standing biomass (Fuller *et al.* 1985; Bazely & Jefferies 1986; Evers *et al.* 1998) and litterfall (Pastor *et al.* 1993) such that litter inputs to the soil are reduced in grazed areas. In contrast, at Susitna Flats litter inputs to the soil are greater on grazed areas due to trampling, which results in less litter accumulation on the soil surface.

EFFECTS OF GEESE ON FORAGE AVAILABILITY

Feeding by Canada and snow geese had no effect on forage availability in the sedge meadow community, but reduced the availability of some forage species in the herb meadow community. Of particular importance to snow geese was a 29% reduction in *Plantago* in grazed areas compared to exclosed after three years of fencing, as this species was 40% of the snow goose diet. The 21% reduction in biomass of *Puccinellia* in grazed areas after three years probably impacted Canada geese, as this forage composed 28% of their diet.

In contrast, *Triglochin*, comprising 20% and 30% of snow goose and Canada goose diets respectively, was not affected by feeding. There was 59% more *C. ramenskii*, an important part of snow (20%) and Canada (16%) goose diets, in grazed areas compared to exclosed after three years. The species on which herbivory had the greatest effect, *Potentilla*, was not a forage plant for either goose species. However, the decrease

in *Potentilla* on grazed plots may have reduced competitive pressure on other species (particularly *C. ramenskii*), and indirectly resulted in increased forage availability.

C. ramenskii and *Triglochin* may fill gaps in both snow goose and Canada goose diets left by reduced availability of *Plantago* and *Puccinellia*. However, *C. ramenskii*, *Triglochin*, and *Plantago* differ in nitrogen, acid detergent fibre, and non-structural carbohydrate content in early spring (A. Zacheis, unpublished data). Therefore, although the quantity of forage available to geese may be unaltered by goose activity, we do not know how the overall quality of the diet is affected.

Negative effects of geese on forage availability do not appear to be cumulative. The differences in *Plantago* and *Puccinellia* biomass between grazed and exclosed plots did not increase over the three years of the study. This indicates that the marsh is not rapidly deteriorating as habitat for either goose species due to grubbing, probably because foraging pressure is light and spatially variable among years.

Conclusion

This study illustrates that even light or ephemeral herbivore pressure can alter plant communities and the availability of forage plants for the consumer. However, communities respond to herbivory differently, and the tolerance of plant species to herbivory, as well as the type of herbivory, may be important in determining community response. In this marsh, grubbing for below-ground biomass of *Plantago* by snow geese appears to cause shifts in relative species abundance in the herb meadow community. Finally, the response of an individual plant species to herbivory is dependent on the

community in which it is growing, suggesting that herbivores alter competitive interactions between plant species.

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References

- Abraham, K.F. & Jefferies, R.L. (1997) High goose populations: causes, impacts and implications. *Arctic Goose Habitat Working Group Report* (ed. B. Batt), pp. 7-72. Arctic Goose Joint Venture Special Publication, U.S. Fish and Wildlife Service, Washington, D.C., and Canadian Wildlife Service, Ottawa, Ontario.
- Ankney, C.D. (1996) An embarrassment of riches: too many geese. *Journal of Wildlife Management*, **60**, 217-223.
- Archer, S. & Smeins, F.E. (1991) Ecosystem-level processes. *Grazing Management. An Ecological Perspective* (eds. R.K. Heitschmidt & J.W. Stuth), pp. 109-139. Timber Press, Portland, Oregon.
- Archer, S.R. & Tieszen, L.L. (1986) Plant responses to defoliation: hierarchical considerations. *Grazing Research at Northern Latitudes* (ed. O. Gudmundson), pp. 45-59. Plenum Press, New York, New York.
- Bazely, D.R. & Jefferies, R.L. (1986) Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *Journal of Ecology*, **74**, 693-706.
- Bazely, D.R. & Jefferies, R.L. (1989) Leaf and shoot demography of an arctic stoloniferous grass, *Puccinellia phryganodes*, in response to grazing. *Journal of Ecology*, **77**, 811-822.
- Beaulieu, J., Gauthier, G. & Rochefort, L. (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology*, **84**, 905-914.

- Bélangier, L. & Bédard, J. (1994) Role of ice scouring and goose grubbing in marsh plant dynamics. *Journal of Ecology*, **82**, 437-445.
- Bélangier, L., Giroux, J.-F. & Bédard, J. (1990) Effects of goose grazing on the quality of *Scirpus americanus* rhizomes. *Canadian Journal of Zoology*, **68**, 1012-1014.
- Ben-Ari, E.T. (1998) A new wrinkle in wildlife management. *BioScience*, **48**, 667-673.
- Biondini, M.E., Patton, B.D. & Nyren, P.E. (1998) Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. *Ecological Applications*, **8**, 469-479.
- Butler, W.I. Jr. & Gill, R.E. (1987) *Spring 1986 Aerial Surveys of Geese and Swans Staging in Upper Cook Inlet*. U.S. Fish and Wildlife Service, Anchorage, Alaska.
- Cargill, S.M. & Jefferies, R.L. (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 669-686.
- Conover, W.J. (1980) *Practical Nonparametric Statistics*, 2nd edn. John Wiley & Sons, New York, New York.
- Cooch, E.G. & Cooke, F. (1991) Demographic changes in a Snow Goose population: biological and management implications. *Bird Population Studies: Relevance to Conservation and Management* (eds. C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 168-189. Oxford University Press, Oxford.
- Cooke, F., Rockwell, R.F. & Lank, D.B. (1995) *The Snow Geese of La Pérouse Bay*. Oxford University Press, Oxford.
- Crawley, M.J. (1983) *Herbivory*. University of California Press, Berkeley, California.

- Crawley, M.J. (1990) Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology*, **27**, 803-820.
- Crawley, M.J. (1997) Plant-herbivore dynamics. *Plant Ecology* (ed. M.J. Crawley), pp. 401-474. Blackwell Science, Oxford.
- Dormann, C.F., Van der Wal, R. & Bakker, J.P. (2000) Competition and herbivory during salt marsh succession: the importance of forb growth strategy. *Journal of Ecology*, **88**, 571-583.
- Esselink, P., Helder, G.J.F., Aerts, B.A. & Gerdes, K. (1997) The impact of grubbing by Greylag Geese (*Anser anser*) on the vegetation dynamics of a tidal marsh. *Aquatic Botany*, **55**, 261-279.
- Evers, D.E., Sasser, C.E., Gosselink, J.G., Fuller, D.A. & Visser, J.M. (1998) The impact of vertebrate herbivores on wetland vegetation in Atchafalaya Bay, Louisiana. *Estuaries*, **21**, 1-13.
- Ford, M.A. & Grace, J.B. (1998) Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. *Journal of Ecology*, **86**, 974-982.
- Fuller, D.A., Sasser, C.E., Johnson, W.B. & Gosselink, J.G. (1985) The effects of herbivory on vegetation on islands in Atchafalaya Bay, Louisiana. *Wetlands*, **4**, 105-114.
- Furbish, C.E. & Albano, M. (1994) Selective herbivory and plant community structure in a mid-Atlantic salt marsh. *Ecology*, **75**, 1015-1022.

- Ganter, B., Cooke, F. & Mineau, P. (1996) Long-term vegetation changes in a Snow Goose nesting habitat. *Canadian Journal of Zoology*, **74**, 965-969.
- Gauthier, G., Hughes, R.J., Reed, A., Beaulieu, J. & Rochefort, L. (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653-664.
- Giroux, J.-F. & Bédard, J. (1987) The effects of grazing by greater snow geese on the vegetation of tidal marshes in the St. Lawrence estuary. *Journal of Applied Ecology*, **24**, 773-788.
- Giroux, J.-F. & Bédard, J. (1988) Use of bulrush marshes by greater snow geese during staging. *Journal of Wildlife Management*, **52**, 415-420.
- Hik, D.S. & Jefferies, R.L. (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *Journal of Ecology*, **78**, 180-195.
- Hik, D.S., Sadul, H.A. & Jefferies, R.L. (1991) Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. *Journal of Ecology*, **79**, 715-730.
- Hultén, E. (1968) *Flora of Alaska and Neighboring Territories*. Stanford University Press, Stanford, California.
- Inouye, R.S., Byers, G.S. & Brown, J.H. (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology*, **61**, 1344-1351.

- Jano, A.P., Jefferies, R.L. & Rockwell, R.F. (1998) The detection of vegetational change by multitemporal analysis of LANDSAT data: the effects of goose foraging. *Journal of Ecology*, **86**, 93-99.
- Jefferies, R.L. (1988) Vegetational mosaics, plant-animal interactions and resources for plant growth. *Plant Evolutionary Biology* (eds. L.D. Gottlieb & S.K. Jain), pp. 341-369. Chapman and Hall, London.
- Johnson, R.A. & Wichern, D.W. (1992) *Applied Multivariate Statistical Analysis*, 3rd edn. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
- Kerbes, R.H., Baranyuk, V.V. & Hines, J.E. (1999) Estimated size of the Western Canadian Arctic and Wrangel Island lesser snow goose populations on their breeding and wintering grounds. *Distribution, Survival, and Numbers of Lesser Snow Geese of the Western Canadian Arctic and Wrangel Island, Russia* (eds. R.H. Kerbes, K.M. Meeres & J.E. Hines), pp.25-37. Canadian Wildlife Service Occasional Paper 98, Ottawa, Ontario.
- Kerbes, R.H., Kotanen, P.M. & Jefferies, R.L. (1990) Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology*, **27**, 242-258.
- King, J.G. & Derksen, D.V. (1986) Alaska goose populations: past, present and future. *Transactions of the 51st North American Wildlife & Natural Resources Conference*, **51**, 464-479.
- Kotanen, P. & Jefferies, R.L. (1987) The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. *Journal of Ecology*, **75**, 961-975.

- Kotanen, P.M. & Jefferies, R.L. (1997) Long-term destruction of sub-arctic wetland vegetation by lesser snow geese. *Écoscience*, **4**, 179-182.
- McNaughton, S.J., Ruess, R.W. & Seagle, S.W. (1988) Large mammals and process dynamics in African ecosystems. *BioScience*, **38**, 794-800.
- Miller, D.L., Smeins, F.E. & Webb, J.W. (1996) Mid-Texas coastal marsh change (1939-1991) as influenced by lesser snow goose herbivory. *Journal of Coastal Research*, **12**, 462-476.
- Neter, J., Wasserman, W. & Kutner, M.H. (1990) *Applied Linear Statistical Models*, 3rd edn. Irwin, Homewood, Illinois.
- Newman, J.A., Bergelson, J. & Grafen, A. (1997) Blocking factors and hypothesis tests in ecology: is your statistics text wrong? *Ecology*, **78**, 1312-1320.
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. & Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, **74**, 467-480.
- Person, B.T., Babcock, C.A. & Ruess, R.W. (1998) Forage variation in brood-rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska. *Journal of Ecology*, **86**, 243-259.
- Prevett, J.P., Marshall, I.F. & Thomas, V.G. (1985) Spring foods of snow and Canada geese at James Bay. *Journal of Wildlife Management*, **49**, 558-563.
- Prins, H.H.Th., Ydenberg, R.C. & Drent, R.H. (1980) The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. *Acta Botanica Neerlandica*, **29**, 585-596.

- Rosenthal, J.P. & Kotanen, P.M. (1994) Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution*, **9**, 145-148.
- Ruess, R.W., Uliassi, D.D., Mulder, C.P.H. & Person, B.T. (1997) Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: Implications for geese-ecosystem dynamics in western Alaska. *Écoscience*, **4**, 170-178.
- Smith, T.J. III (1983) Alteration of salt marsh plant community composition by grazing snow geese. *Holarctic Ecology*, **6**, 204-210.
- Smith, T.J. III & Odum, W.E. (1981) The effects of grazing by snow geese on coastal salt marshes. *Ecology*, **62**, 98-106.
- Snow, A.A. (1982) *Plant zonation in an Alaskan salt marsh: an experimental study of the role of edaphic conditions*. PhD thesis, University of Massachusetts, Amherst, Massachusetts.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman and Company, New York, New York.
- Srivastava, D.S. & Jefferies, R.L. (1996) A positive feedback: herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. *Journal of Ecology*, **84**, 31-42.
- Swanson, G.A., Krapu, G.L., Bartonek, J.C., Serie, J.R. & Johnson, D.H. (1974) Advantages in mathematically weighting waterfowl food habits data. *Journal of Wildlife Management*, **38**, 302-307.

- Vince, S.W. & Snow, A.A. (1984) Plant zonation in an Alaskan salt marsh. I. Distribution, abundance and environmental factors. *Journal of Ecology*, **72**, 651-667.
- Van Wijnen, H.J., Van der Wal, R. & Bakker, J.P. (1999) The impact of herbivores on nitrogen mineralization rate: consequence for salt-marsh succession. *Oecologia*, **118**, 225-231.
- Wilkens, K.A. & Cooch, E.G. (1999) *Waterfowl Population Status, 1999*. U.S. Fish & Wildlife Service, Washington D.C.
- Williams, T.D., Cooch, E.G., Jefferies, R.L. & Cooke, F. (1993) Environmental degradation, food limitation and reproductive output: juvenile survival in lesser snow geese. *Journal of Animal Ecology*, **62**, 766-777.
- Youngner, V.B. (1972) Physiology of defoliation and regrowth. *The Biology and Utilization of Grasses* (eds. V.B. Youngner & C.M. McKell), pp. 292-303. Academic Press, New York, New York.
- Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, New Jersey.
- Zellmer, I.D., Clauss, M.J., Hik, D.S. & Jefferies, R.L. (1993) Growth responses of arctic graminoids following grazing by captive lesser snow geese. *Oecologia*, **93**, 487-492.

Table 1.1 Plant species composition, soil characteristics, and flooding regime of the sedge meadow and herb meadow communities in Susitna Flats, Alaska. Plant species composition is based on biomass measured on grazed plots in 1994, before exclosure treatments were applied (n=16 for the sedge meadow and n=72 for the herb meadow). Soil properties were measured in 1997 on grazed plots (n=16 for the sedge meadow and n=24 for the herb meadow). Soil moisture and salinity are the means of three and two measurements, respectively, taken throughout the growing season. Other soil properties were measured in May. Data are means \pm 1 SE.

	Sedge meadow		Herb meadow	
Plant species	<i>Carex ramenskii</i>	42.4 \pm 6.7%	<i>Triglochin maritimum</i>	50.9 \pm 2.5%
	<i>Triglochin maritimum</i>	56.9 \pm 6.8%	<i>Plantago maritima</i>	13.0 \pm 2.2%
	Other forbs and grasses	0.7 \pm 0.7%	<i>Potentilla egedii</i>	8.2 \pm 1.1%
			<i>Carex ramenskii</i>	20.5 \pm 2.7%
			Other forbs, grasses, sedges	7.4 \pm 1.2%
Soil moisture	35.67 \pm 0.41%		30.40 \pm 0.47%	
Soil salinity	14.97 \pm 0.82‰		12.07 \pm 0.45‰	
Soil organic matter	3.39 \pm 0.15%		3.51 \pm 0.17%	
Soil pH	7.25 \pm 0.04		7.33 \pm 0.02	
Plot distance from coast	25 – 350 m		75 m – 1 km	
Flooding regime	monthly high tides		storm tides and extreme high tides	

Table 1.2 Response of the sedge and herb meadow communities to goose herbivory, Susitna Flats, Alaska, 1995-97. *F*-values from repeated measures MANOVA analyses are reported. Treatment effect compares plots fed on by geese (grazed) with plots exclosed from goose use. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

			F-values		
Community/ Plant species	Source of variation	d.f.	Above-ground biomass	Plant density	Inflorescence density
Sedge Meadow Community					
<i>Carex</i>	Treatment	1, 15	0.04	0.28	4.94*
<i>ramenskii</i>	Year	2, 14	1.10	4.57* ^a	10.88*** ^a
	Year*Treatment	2, 14	0.10	0.67 ^a	0.42 ^a
<i>Triglochin</i>	Treatment	1, 15	0.14	1.45	2.71
<i>maritimum</i>	Year	2, 14	8.91**	0.41 ^a	170.91***
	Year*Treatment	2, 14	0.71	0.04 ^a	0.12
Total	Treatment	1, 15	0.02	2.19	8.27*
Live	Year	2, 14	14.77***	6.79* ^a	23.88*** ^a
	Year*Treatment	2, 14	0.31	0.13 ^a	0.80 ^a

Standing	Treatment	1, 15
Dead	Year	2, 14
	Year*Treatment	2, 14

Litter	Treatment	1, 15
	Year	1, 15
	Year*Treatment	1, 15

Herb Meadow Community

<i>Triglochin</i>	Treatment	1, 71
<i>maritimum</i>	Year	2, 70
	Year*Treatment	2, 70

<i>Plantago</i>	Treatment	1, 71
<i>maritima</i>	Year	2, 70
	Year*Treatment	2, 70

<i>Potentilla</i>	Treatment	1, 71
<i>egedii</i>	Year	2, 70
	Year*Treatment	2, 70

0.69	---	---
2.41	---	---
1.43	---	---
8.61**	---	---
10.67**	---	---
0.14	---	---
0.02	2.93	2.40
22.85***	5.69* ^b	281.39***
0.18	2.66 ^b	1.04
4.20*	5.01*	3.12
9.28***	122.79*** ^b	34.47***
0.47	0.76 ^b	4.55*
9.94**	21.58***	21.01***
9.83***	85.37*** ^b	6.63**
6.15**	0.22 ^b	4.75*

<i>Puccinellia</i>	Treatment	1, 71
spp.	Year	2, 70
	Year*Treatment	2, 70
<i>Carex</i>	Treatment	1, 71
<i>ramenskii</i>	Year	2, 70
	Year*Treatment	2, 70
Total	Treatment	1, 71
Live	Year	2, 70
	Year*Treatment	2, 70
Standing	Treatment	1, 71
Dead	Year	2, 70
	Year*Treatment	2, 70
Litter	Treatment	1, 71
	Year	1, 71
	Year*Treatment	1, 71

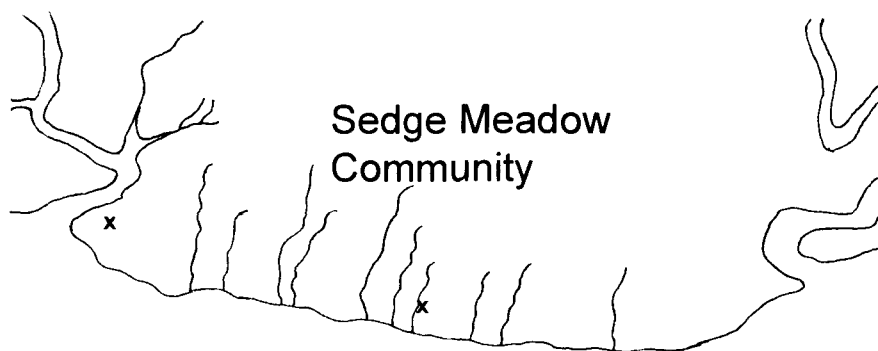
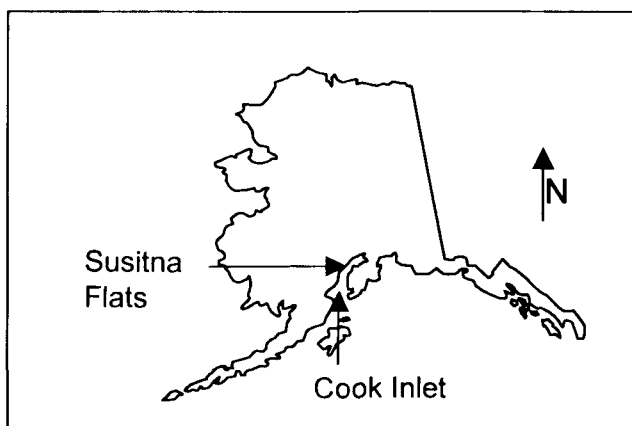
^a d.f. 1, 15 ^b d.f. 1, 71

4.60*	---	---
25.02***	---	---
0.14	---	---
11.95***	36.34***	14.10***
44.40***	4.57* ^b	17.33*** ^b
2.10	3.59 ^b	8.77** ^b
2.53	1.17	0.07
42.18***	92.94*** ^b	12.13*** ^b
0.41	1.82 ^b	4.89* ^b
9.40**	---	---
189.42***	---	---
3.23*	---	---
38.95***	---	---
16.18***	---	---
3.27	---	---

Table 1.3 Pearson correlation coefficients between *Carex ramenskii* biomass and *Plantago maritima*, *Potentilla egedii*, and *Puccinellia* spp. biomass within the herb meadow community, Susitna Flats, Alaska, for 1994 (pre-treatment year) through 1997. Significance values are based on log transformed data. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

			<i>Plantago maritima</i>	<i>Potentilla egedii</i>	<i>Puccinellia spp.</i>
1994	<i>Carex ramenskii</i>	all plots	-0.618***	-0.347***	-0.260**
		exclosed plots only	-0.609***	-0.174	-0.212
1995	<i>Carex ramenskii</i>	all plots	-0.505***	-0.227**	-0.363***
		exclosed plots only	-0.588***	-0.201	-0.387***
1996	<i>Carex ramenskii</i>	all plots	-0.465***	-0.226**	-0.297***
		exclosed plots only	-0.503***	-0.195	-0.332**
1997	<i>Carex ramenskii</i>	all plots	-0.493***	-0.215**	-0.292***
		exclosed plots only	-0.504***	-0.195	-0.188

Figure 1.1 Location of plant communities and study sites at Susitna Flats, Alaska. Transect locations are denoted with an x.



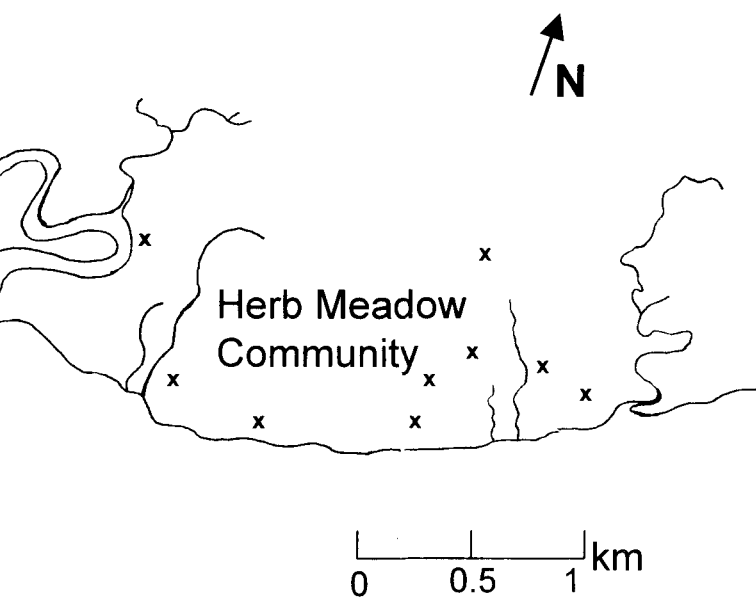
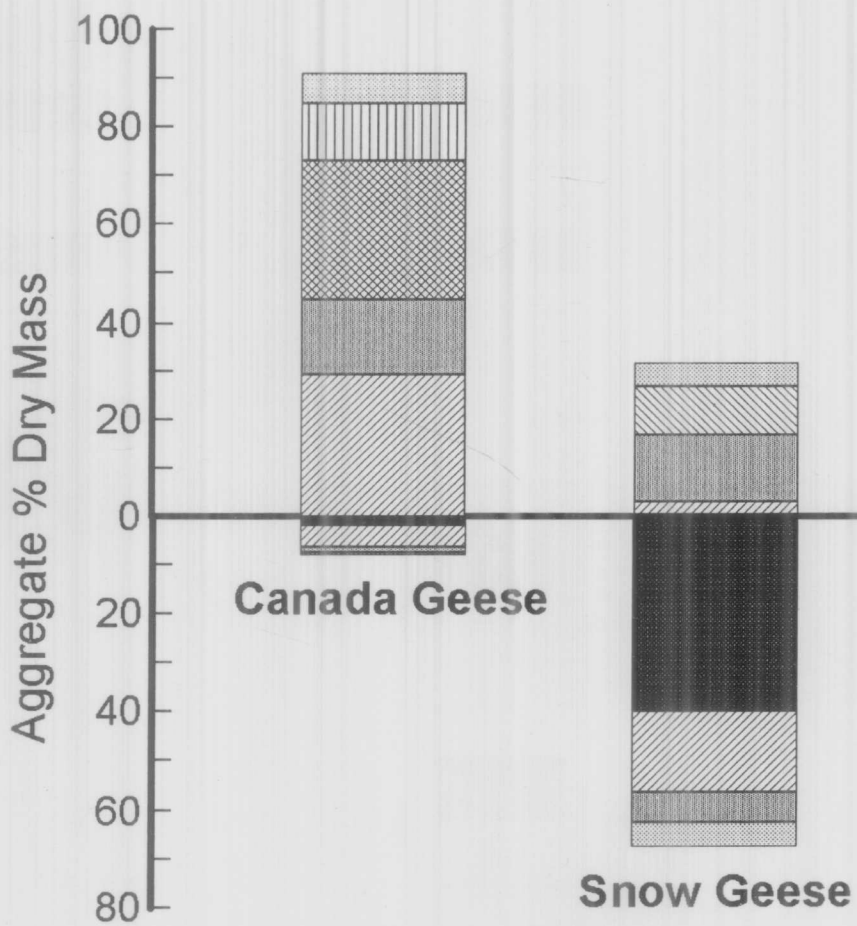









Figure 1.2 Aggregate percent dry mass of forage items in oesophagi of snow and Canada geese ($n = 45$ and 28 , respectively) collected in Upper Cook Inlet, Alaska, April 1996-98.



-  Other
-  Seeds
-  *Carex lyngbyaei*
-  *Puccinellia* spp.
-  *Carex ramenskii*
-  *Triglochin maritimum*
-  *Plantago maritima*

Above-ground

Below-ground

Figure 1.3 Biomass response of the sedge meadow community to goose herbivory, Susitna Flats, Alaska, 1995-97. Comparison of plots grazed by geese and those exclosed from geese for (a) *Carex ramenskii* biomass, (b) *Triglochin maritimum* biomass, (c) total above-ground live biomass, (d) standing dead material, and (e) litter. Litter was measured in 1996 and 1997 only. Note different y-axis scales.

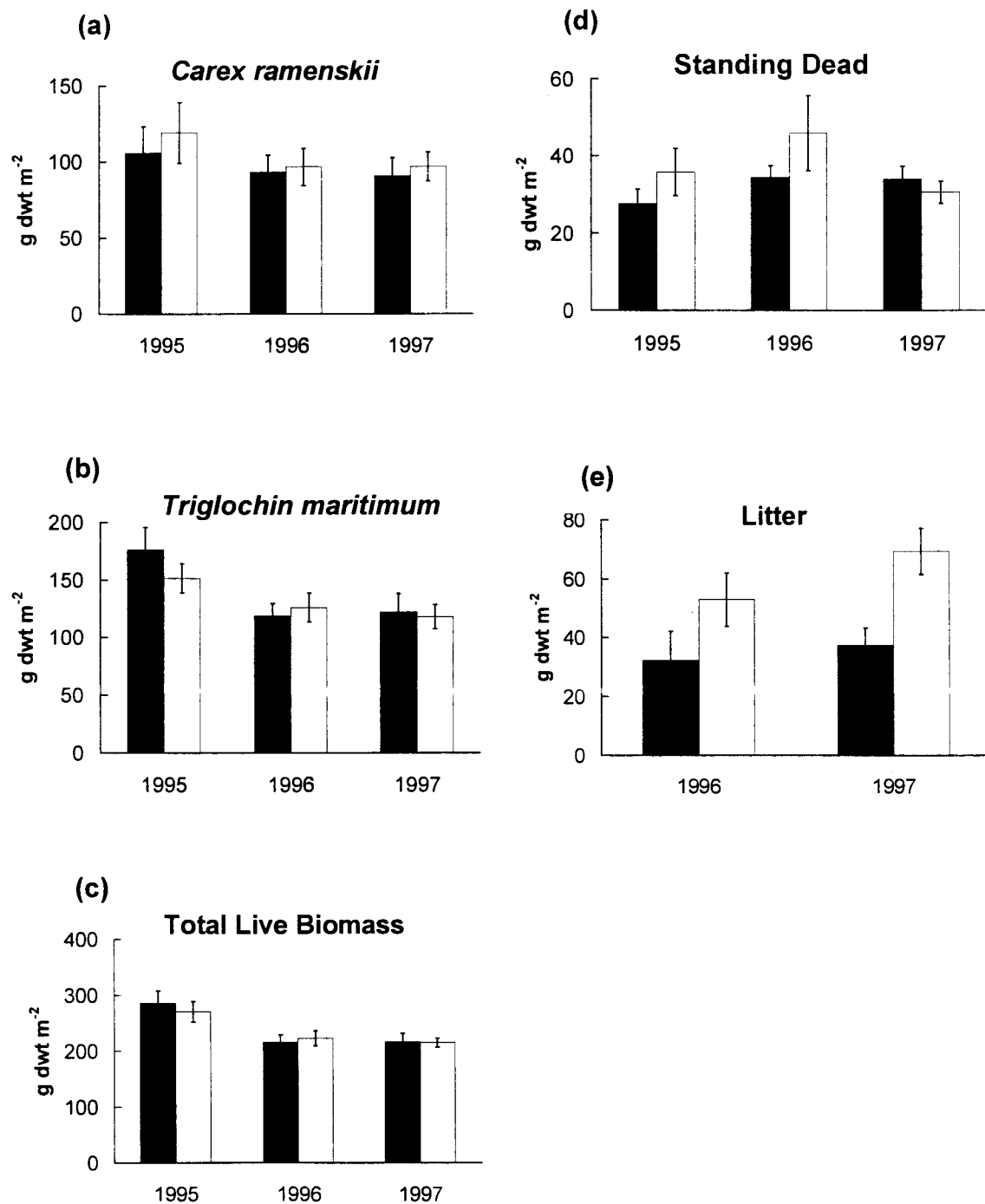
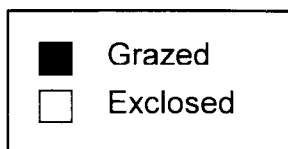


Figure 1.4 Plant density response of the sedge meadow community to goose herbivory, Susitna Flats, Alaska, 1995-97. Comparison of plots grazed by geese and those exclosed from geese for (a) *Carex ramenskii* plant density, (b) *Triglochin maritimum* plant density, (c) total plant density, (d) *Carex ramenskii* inflorescence density, (e) *Triglochin maritimum* inflorescence density, and (f) total inflorescence density. Plant density and *Carex ramenskii* inflorescence density were measured in 1996 and 1997 only. Note different y-axis scales.

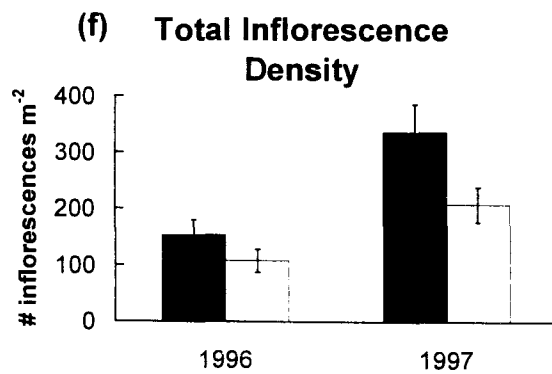
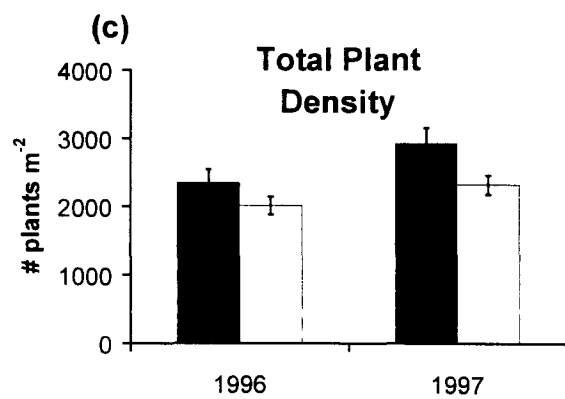
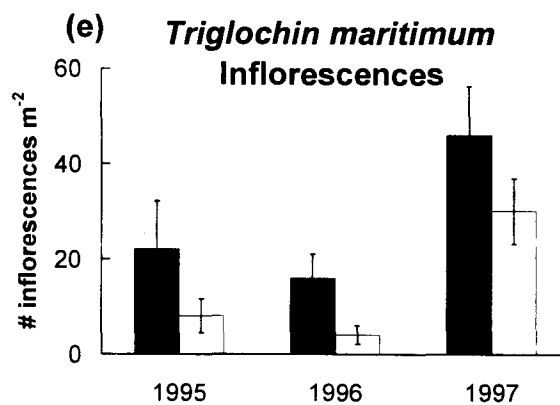
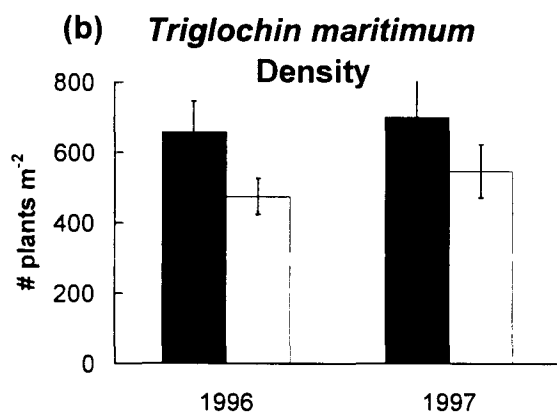
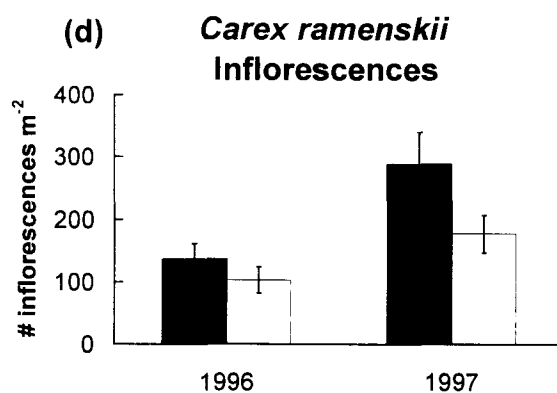
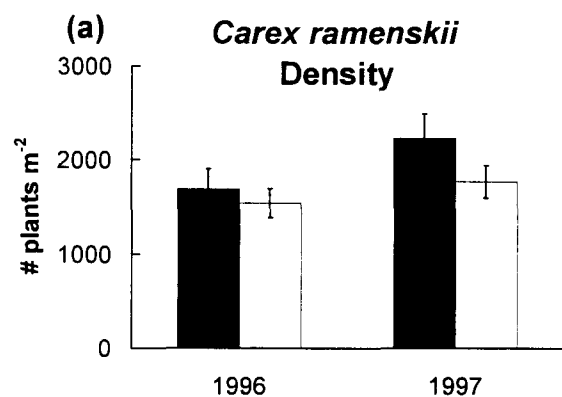
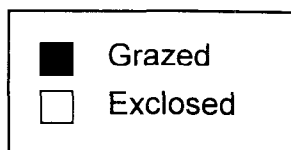


Figure 1.5 Biomass response of the herb meadow community to goose herbivory, Susitna Flats, Alaska, 1995-97. Comparison of plots grazed by geese and those exclosed from geese for (a) *Triglochin maritimum* biomass, (b) *Plantago maritima* biomass, (c) *Potentilla egedii* biomass, (d) *Puccinellia* spp. biomass, (e) *Carex ramenskii* biomass, (f) total above-ground live biomass, (g) standing dead material, and (h) litter. Litter was measured in 1996 and 1997 only. Note different y-axis scales.

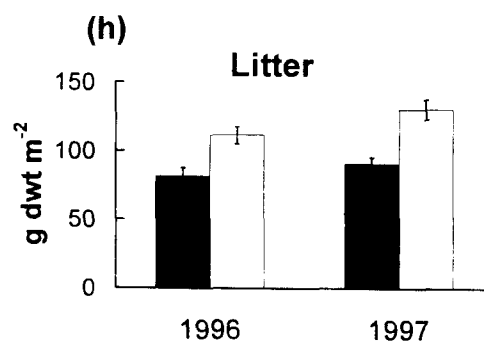
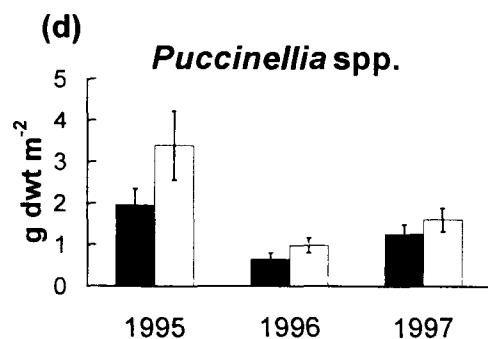
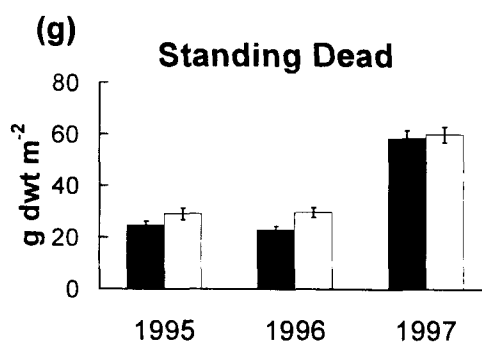
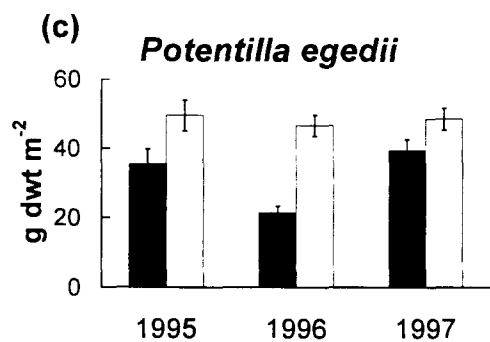
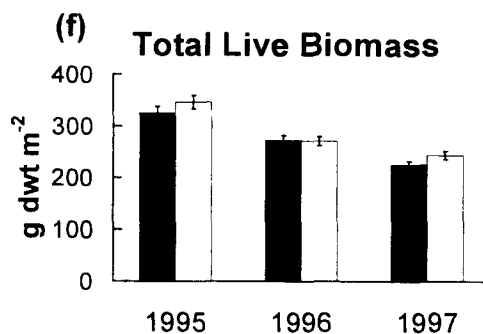
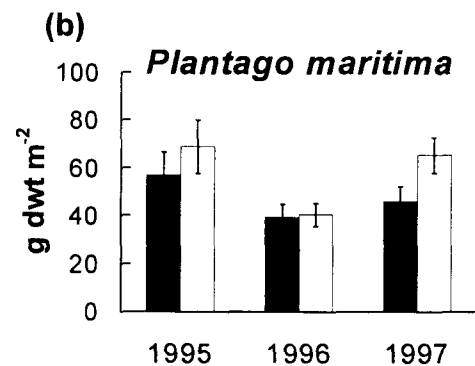
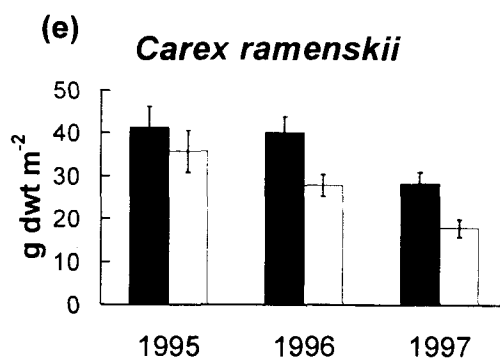
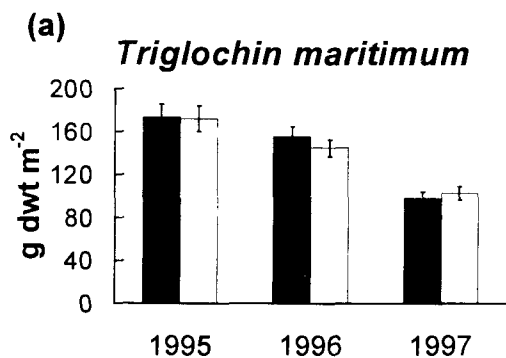
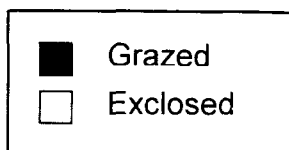
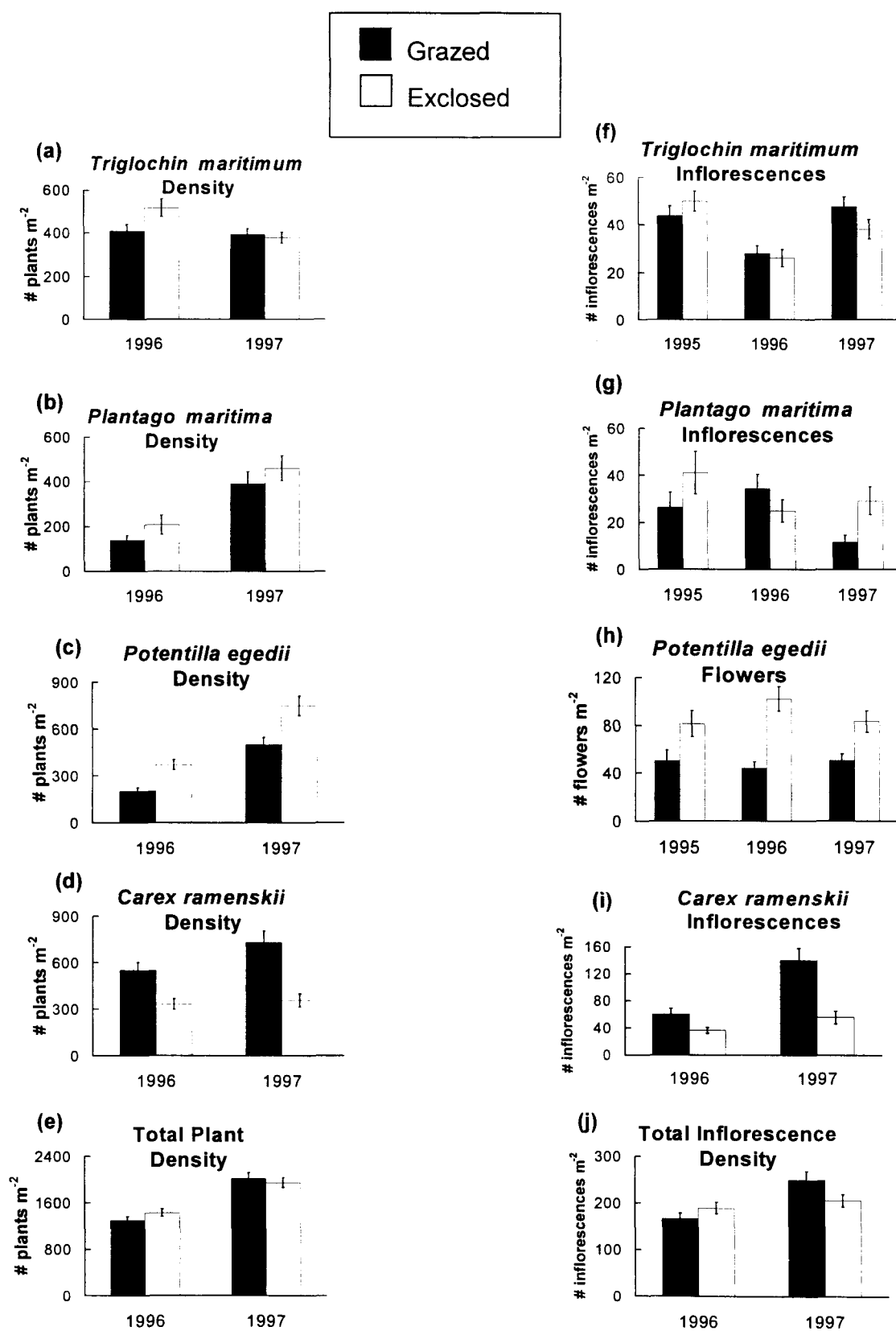


Figure 1.6 Plant density response of the herb meadow community to goose herbivory, Susitna Flats, Alaska, 1995-97. Comparison of plots grazed by geese and those exclosed from geese for (a) *Triglochin maritimum* plant density, (b) *Plantago maritima* plant density, (c) *Potentilla egedii* plant density, (d) *Carex ramenskii* plant density, (e) total plant density, (f) *Triglochin maritimum* inflorescence density, (g) *Plantago maritima* inflorescence density, (h) *Potentilla egedii* flower density, (i) *Carex ramenskii* inflorescence density, and (j) total inflorescence density. Plant density and *Carex ramenskii* inflorescence density were measured in 1996 and 1997 only. Note different y-axis scales.



EFFECTS OF MIGRATORY GEESE ON NITROGEN DYNAMICS IN AN ALASKAN SALT MARSH²

ABSTRACT

Lesser snow geese (*Anser caerulescens caerulescens*) and Canada geese (*Branta canadensis*) use several salt marshes in Cook Inlet, Alaska, as stopover areas for brief periods during spring migration. We investigated the effects of geese on nitrogen cycling processes in two plant communities within Susitna Flats, one of the marshes. We compared net nitrogen mineralization, organic nitrogen pools and production in buried bags, microbial nitrogen, nitrogen fixation by cyanobacteria, and soil and plant characteristics on paired grazed and exclosed plots during the 1997 growing season.

In the sedge meadow community, grazed areas had higher rates of net nitrogen mineralization in the spring, although there was no effect of grazing on organic nitrogen availability or on microbial biomass nitrogen. The increased mineralization rates in grazed plots could not be accounted for by alteration of litter quality, litter quantity, microclimate, or root biomass, which were not different between grazed and exclosed plots. In addition, fecal input was very slight. We propose that trampling had two effects that could account for greater nitrogen availability in grazed areas: litter incorporation into soils, resulting in increased rates of decomposition and mineralization of

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organic nitrogen in litter, and greater rates of nitrogen fixation by cyanobacteria on bare, trampled soils. A path analysis indicated that litter incorporation played a primary role in nitrogen dynamics of the system, with nitrogen fixation secondary, and fecal input of little importance. Greater net nitrogen mineralization rates in grazed areas did not result in higher nitrogen concentrations in plants or in higher quality diets for geese.

In the herb meadow community, there was no detectable effect of grazing on organic or inorganic nitrogen availability. Soils were drier than in the sedge meadow, with little standing water, and use by geese was much lighter, so that incorporation of litter into soils through trampling may have been less important.

Key words: Alaska, geese, herbivory, microbial nitrogen, net nitrogen mineralization, nitrogen cycling, nitrogen fixation, organic nitrogen, plant litter, plant nitrogen, salt marsh, trampling.

INTRODUCTION

Herbivores and other animals can affect nitrogen availability to plants by providing a readily accessible form of nitrogen in excreta (Floate 1981, Bazely and Jefferies 1985, Thomas et al. 1988, Day and Detling 1990, Thomas et al. 1990, Ben-David et al. 1998) or by altering net nitrogen mineralization rates in soils (e.g., Holland and Detling 1990, Pastor et al. 1993, McNaughton et al. 1997, Biondini et al. 1998, Frank and Groffman 1998, Sirotnak and Huntly 2000). Changing the availability of nitrogen in ecosystems where nitrogen is limited can impact microbial and plant communities, and ultimately affect herbivores if the quality and/or abundance of forage are altered (Bazely

and Jefferies 1985, Day and Detling 1990). Several mechanisms explaining differences in plant tissue nitrogen concentrations or in net nitrogen mineralization rates between grazed and ungrazed areas have been suggested (e.g., Bazely and Jefferies 1985, McNaughton et al. 1988, Holland and Detling 1990, Pastor et al. 1993, van Wijnen et al. 1999, Sirotnak and Huntly 2000). We propose that trampling of plant litter, a previously untested mechanism potentially affecting nitrogen availability, can increase net nitrogen mineralization, primarily through the incorporation of litter into soils.

The addition of feces and urine or uric acid alone, without grazing, has been shown to result in increased plant nitrogen concentration in some grazing systems (Bazely and Jefferies 1985, Thomas et al. 1986, Thomas et al. 1988, Day and Detling 1990, Ben-David et al. 1998). In contrast, fecal additions to soil may increase (Pastor et al. 1993, Zaady et al. 1996) or decrease rates of net nitrogen mineralization (Ruess and McNaughton 1987, Seagle et al. 1992) over unamended soils. However, in many systems, excretory nitrogen from herbivores is a minor input or is too patchily distributed to significantly affect nitrogen dynamics (Floate 1981, Pastor et al. 1993). Instead, herbivores can affect nitrogen mineralization by altering, for example, the quality of litter for decomposition. Grazing can increase plant nitrogen uptake per unit root biomass, resulting in higher shoot nitrogen concentrations (Ruess et al. 1983, Jaramillo and Detling 1988, Polley and Detling 1989), and maintain plants in a juvenile form with lower shoot C:N ratios (Coppock et al. 1983, Ruess 1987, Whicker and Detling 1988). This results in higher quality litter (lower C:N ratio) for decomposition, higher quality soil organic matter, and higher rates of net nitrogen mineralization in grazed areas (Sirotnak and

Huntly 2000). Conversely, selective grazing on palatable plant species can reduce their abundance and give a competitive advantage to less palatable (higher C:N ratio) species, resulting in more recalcitrant litter in grazed areas, and in lower rates of net nitrogen mineralization or in reduced nitrogen availability (Pastor et al. 1988, Pastor et al. 1993, Ritchie et al. 1998, Sirotinak and Huntly 2000).

Herbivores also affect nitrogen mineralization by reducing litter and root production. Browsed or grazed vegetation may have less root biomass (Youngner 1972) or lower rates of fine root production (Ruess et al. 1998), which may result in reduced carbon flow to decomposers and less microbial immobilization of nitrogen (Holland and Detling 1990, Holland et al. 1992). Reduction of litter biomass, commonly seen in grazed areas as primary production and/or peak biomass is reduced (Coppock et al. 1983, Bazely and Jefferies 1986, McNaughton et al. 1988, Pastor et al. 1993, Biondini et al. 1998, van Wijnen et al. 1999), is correlated with lower rates of net nitrogen mineralization (Pastor et al. 1993, Biondini et al. 1998, van Wijnen et al. 1999), as there is less substrate available for decomposition (Pastor et al. 1984). Finally, animals can increase the availability of inorganic nitrogen by digging and disturbing soil (Tardiff and Stanford 1998) and, potentially, by altering microclimate and thus mineralization rates (Dormaar et al. 1990, Frank and Groffman 1998).

It has been suggested that trampling by animals may accelerate decomposition by fragmenting plant material and incorporating it into soil (Floate 1981, Ruess 1987, McNaughton et al. 1988, Manley et al. 1995), increasing both the surface area and proximity of plant material to decomposers. Increased rates of decomposition would

reduce the carbon and nitrogen held in the slowly decomposing litter compartment (House et al. 1984, McNaughton et al. 1988, Manley et al. 1995), increase substrate availability to microbes, and speed the cycling of nitrogen through a system. In addition, trampling reduces the litter layer, facilitating the growth of nitrogen-fixing cyanobacteria, which grow preferentially on bare salt marsh soils (Bazely and Jefferies 1989). However, the idea that trampling, separate from other effects of herbivores, can increase nitrogen availability within an ecosystem has not been previously investigated.

We studied the effects of lesser snow geese (*Anser caerulescens caerulescens* L.) and Canada geese (*Branta canadensis* L.) on nitrogen cycling in a salt marsh in Cook Inlet, Alaska, used by the geese as a stopover area during spring migration. Several characteristics of this system made it well suited for the comparison of trampling effects with other potential effects of herbivores on nitrogen availability. Geese only exploited salt marsh habitats in early spring when plant growth was minimal. Flocks typically remained at feeding sites for only 10-25 days (Hupp et al., *in press*, Zacheis et al., *in press*) and did not revisit the area until the following spring. Because the duration of use was short and plants were grazed at an early stage of development, late summer standing crop was not affected by grazing and annual litter production was similar between grazed and ungrazed areas (Zacheis et al., *in press*). However, due to flocking behavior of geese, grazed areas were heavily trampled in spring resulting in a nearly complete lack of litter on the soil surface after birds departed from the marsh. Fecal input to the system was very low in 1997, allowing us to more clearly isolate the effects of trampling on nutrient availability. Finally, wetland soils had a low organic matter content, so that litter

inputs from trampling were not masked by nutrient contributions from a large pool of previously existing organic material.

The objectives of the study were (i) to determine if geese affect nitrogen availability to plants, and if so, under what conditions; (ii) to compare trampling effects with other potential effects of geese on nitrogen availability; (iii) to determine if an increase in nitrogen availability resulted in higher plant tissue nitrogen concentrations; and (iv) to determine whether any alterations in forage quality feed back into changes in diet quality for geese.

METHODS

Study site

We conducted this study in Susitna Flats, a 100 km² salt marsh in Cook Inlet, Alaska (61°15' N, 150°30' W) (Fig. 1). Lesser snow geese and Taverner's (*B. c. taverneri* Delacour) and cackling Canada geese (*B. c. minima* Ridgway) use Cook Inlet as a stopover area during spring migration in April and May. Although 34,000 or more snow geese and 70,000 or more Canada geese may use the marshes (Butler and Gill 1987), grazing intensity is light in Susitna Flats, because birds are in the area for only a short period (Zacheis et al., *in press*). Grazing intensities in 1995 and 1996 were 930 and 1930 goose-days/km², respectively, several orders of magnitude less than other goose staging areas (Zacheis et al., *in press*). Grazing intensity in 1997 was exceptionally light (650 goose-days/km²), with very little use by snow geese (30 goose-days/km²), because many birds apparently bypassed the area owing to dry conditions (Zacheis et al., *in*

press). Because grazing intensity was light in 1997, fecal inputs to marsh soils were very small (averaging 1.3 - 1.8 feces/m²; Zacheis et al., *in press*).

Our study was conducted in two plant communities within Susitna Flats: a sedge meadow and an herb meadow. The sedge meadow was composed almost exclusively of *Carex ramenskii* Kom. and *Triglochin maritimum* L. (nomenclature follows Hultén 1968). The dominant species in the herb meadow were *Triglochin maritimum*, *Potentilla egedii* Wormsk., *Plantago maritima* L., and *Carex ramenskii* (hereafter referred to by genus). There were only a few centimeters of aboveground shoot growth in April and May when geese were present. Canada geese fed primarily on aboveground shoots of *Carex* and *Triglochin*, while snow geese grubbed for roots and rhizomes of *Plantago*, *Triglochin*, and *Carex* (Zacheis et al., *in press*).

Feeding by geese did not affect aboveground peak biomass, belowground biomass or biomass of either of the dominant species in the sedge meadow community after three years of fencing (Zacheis et al., *in press*). In contrast, there was a change in relative species abundance associated with fencing in the herb meadow community, although peak aboveground and belowground biomass were not altered (Zacheis et al., *in press*). There was more *Carex* and less *Plantago* and *Potentilla* in grazed plots compared to ungrazed in the herb meadow. In both communities, there was significantly more litter in ungrazed plots (Zacheis et al., *in press*).

Exclosures

We used a series of paired grazed/exclosed plots to investigate the effects of geese on nitrogen cycling. Details of exclosure set up and design are given in Zacheis et al. (*in press*). Briefly, eight pairs of 1 m² plots were located at 15 m intervals along 11 transects. One randomly selected plot from each pair was exclosed during the spring of 1995, 1996, and 1997; the other plot was left open to grazing. We also set up paired grazed/exclosed "offtake" plots (25 cm x 25 cm) located near each transect of 1 m² plots to measure the amount of forage removed by geese. These were set up in different sites in 1996 and 1997, and maintained at each site for only one spring. All exclosures were constructed of fishing seine, set up before snow melted from plots, and removed after geese left Susitna Flats.

We examined the effects of herbivory on nitrogen cycling on two transects of 1 m² plots in the sedge meadow community (16 pairs of plots) and on three transects in the herb meadow community (24 pairs of plots), with some additional plant and nitrogen fixation sampling on other transects in the herb meadow (Fig. 1). The work was primarily done in 1997, after plots had been exclosed for three consecutive springs. We also sampled vegetation in offtake plots along all 11 transects in the spring of 1996 and 1997, within two weeks of geese departing Susitna Flats.

Net nitrogen mineralization rates

We used buried bags to measure rates of net nitrogen mineralization for three incubation periods throughout the growing season (Eno 1960). Our first incubation

period began May 11-12, about two weeks after geese had left Susitna Flats. The second incubation period began June 12-16, and the third, July 29-August 1. At the beginning of each incubation period we collected paired cylindrical cores 5.5 cm in diameter and 10 cm deep from each of two randomly selected 25 cm x 12.5 cm subplots in each plot. We did not sample in subplots immediately adjacent to previously sampled subplots. Initial NH_4^+ and NO_3^- levels were measured from one core in each pair. We placed the second core of each pair in a polyethylene bag after removing the top 1 cm of soil and vegetation. The bags were sealed, returned to the soil, and the 1 cm soil cap placed on top. Bags were left in place until the start of the subsequent incubation period with final samples from the third incubation period collected by August 28.

We determined soil water content by drying a subsample from each core. We extracted initial and final soil samples with 2N KCl within 48 hours of collection at the field laboratory, and added phenylmercuric acid to inhibit microbial growth. Extracts were frozen at the University of Alaska until analyzed for NH_4^+ -N and NO_3^- -N on a Quikchem AE Automated Ion Analyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Net nitrogen mineralization was the difference in total extractable inorganic nitrogen (NH_4^+ -N plus NO_3^- -N) between final and initial samples, divided by the number of days of incubation.

Extractable organic nitrogen

To determine KCl-extractable organic nitrogen pool sizes and net production in buried bags, we used a Kjeldahl digest procedure on the KCl extracts from the initial and

final buried bag samples collected at each of the three sampling periods. Organic nitrogen pool size was the difference between total extractable nitrogen (NH_4^+ -N plus NO_3^- -N) in the digested samples and extractable inorganic nitrogen (NH_4^+ -N plus NO_3^- -N) in undigested samples. Reported pool sizes are from the initial buried bag samples. Net organic nitrogen production was the final organic nitrogen pool size minus the initial pool size, divided by the number of days of incubation.

Microbial nitrogen

We took 10 cm deep cores from one transect in each of the two plant communities to determine soil microbial nitrogen. Cores were taken in May, June, and July at the same time buried bag incubations were initiated. We sampled two cores from random subplots within each 1 m² plot, kept them cool, and froze them within three days. We later thawed cores, allowed them to sit for three days at room temperature, homogenized them, and removed large roots before we extracted them for microbial nitrogen using a chloroform fumigation extraction technique (Brookes et al. 1985). We divided cores into three sections. One section was fumigated with chloroform for 48 hours, another section immediately extracted with 0.5 N K_2SO_4 , and the third dried for determination of percent soil moisture. Fumigated samples were extracted with K_2SO_4 after repeated evacuation to remove all residual chloroform. Subsamples from each extract were digested with a Kjeldahl procedure and dissolved inorganic nitrogen (NH_4^+ -N plus NO_3^- -N) in both digested and undigested samples was measured on a Quikchem Automated Ion Analyzer. Organic nitrogen was calculated as the difference in nitrogen between digested and

undigested samples, and flush nitrogen as the difference between organic nitrogen in fumigated and non-fumigated samples. We report flush nitrogen values as an index of microbial biomass nitrogen.

Soil characteristics

We measured soil moisture gravimetrically in the initial buried bag samples taken in May, June, and July. We collected additional cores at the same time periods that buried bag samples were initiated for determination of soil properties. We measured bulk density (May, to 10 cm), salinity (May and June, to 10 cm), pH (May, to 10 cm), and total carbon and nitrogen (May and June, to 5 cm; May, June, and July, to 10 cm, one transect per community). Samples were dried at 60 °C to constant weight, ground in a coffee grinder, and passed through a 2 mm mesh sieve. For pH and salinity, a 1:1 soil/distilled water mixture was shaken for 1 hour. We measured pH after the mixture had settled for 1 hour, and salinity 48 hours later, calibrating pH and salinity meters after every four samples. We measured total carbon and nitrogen on a CNS 2000 Elemental Analyzer (LECO Corporation, St. Joseph, Michigan, USA).

We used automatic temperature recording devices (Hobotemp dataloggers, Onset Computer Corporation, Bourne, Massachusetts, USA) to track soil temperature at 3 cm depth during the growing season. Hobotemp probes were buried in randomly selected subplots on two pairs of plots along each transect.

Nitrogen fixation

We used an acetylene reduction assay (Hardy et al. 1968) to estimate nitrogen fixation by cyanobacteria growing on soil surfaces in August 1996, and May and August 1997. We took two 5.5 cm diameter by 5 cm deep cores from randomly selected subplots within each plot and incubated them in 1 liter Mason jars partially buried in the soil. Acetylene was generated from calcium carbide and introduced (~10% v:v) through a septum in the lid. We took samples at 2.5 and 6 hours following acetylene injection, and stored samples in Vacutainer blood collection tubes (Becton, Dickinson and Company, Franklin Lakes, New Jersey, USA) until analysis on a GC-14A gas chromatograph (Shimadzu, Tokyo, Japan) for ethylene. The rate of ethylene production is reported as an index of nitrogen fixation (Hardy et al. 1968).

Plant carbon and nitrogen

We collected peak season biomass on two subplots (25 cm x 12.5 cm) within each 1 m² plot along two transects in the sedge meadow and nine transects in the herb meadow (Fig. 1) in August of 1996 and 1997, after two and three years of fencing, respectively. We also collected shoots of *Triglochin* and *Carex*, and roots and shoots of *Plantago* in offtake plots along all 11 transects in May of 1996 and 1997, after one year of fencing, and within two weeks of geese departing Susitna Flats. Samples were sorted to live, standing dead, and litter, and live samples were sorted by species. Samples were then frozen for transport to the lab, dried at 60 °C to constant weight, ground in a 20-mesh size

Wiley Mill, and combusted for total carbon and nitrogen in a CNS 2000 Elemental Analyzer.

Statistical analysis

We used a repeated measures MANOVA (PROC GLM, SAS v. 8, SAS Institute Inc., Cary, North Carolina, USA), to analyze net nitrogen mineralization rate, organic nitrogen pool size and net production rate, microbial nitrogen, soil moisture, soil salinity, and soil carbon, nitrogen, and C:N ratios. Plant communities were analyzed separately. We used a doubly blocked model, with transects as outer blocks, paired plots nested within transects as inner blocks, and subplots nested within plots. For microbial nitrogen, samples were collected from only one transect per community, so there were no outer blocks in the model. Plot pairs were the replicates on which the repeated measures were made. We tested for treatment effect (exclosure, no exclosure) using the residual mean square error (Newman et al. 1997), but did not test for blocking effects. In addition, if treatment or month x treatment effects were significant, or if error bars indicated significant monthly treatment differences, we analyzed months separately using an ANOVA model with the same doubly blocked design.

The repeated measures MANOVA on the soil temperature data lacked the power to resolve treatment differences because of data lost when Hobotemps malfunctioned or were damaged due to tides, ravens, etc. Therefore, we analyzed these data in PROC MIXED (SAS v.8) which is less sensitive to missing data points (Littell et al. 1996). We ran a repeated measures in PROC MIXED on monthly temperature means, and used an

error structure which allowed correlation between data points (autoregressive order one covariance structure; Littell et al. 1996).

We analyzed soil pH and bulk density, nitrogen fixation rate, and plant carbon, nitrogen, and C:N ratios separately by month or year, with a univariate doubly blocked ANOVA model. For all analyses, we transformed data where necessary ($\log_e + 1$, inverse $+ 1$, or square root $+ 3/8$) to correct for heterogeneous error variance (Neter et al. 1990, Zar 1996). We also ran analyses on ranked data, as transformations could not guarantee that assumptions were met (Conover 1980, Johnson and Wichern 1992). Discrepancies between transformed and ranked analyses are noted in the text. Non-transformed means ± 1 SE are reported throughout.

Path analysis

Path analysis is used to investigate one-way causal models (without feedback loops) through a series of multiple regressions, with the advantage that complex models with several dependent and independent variables can be evaluated (Pedhazur 1982, Mitchell 1993). There are several applications of path analysis, including hypothesis testing, model building, and model description (Mitchell 1993). Path analysis can also be used to break down correlations between variables into causal and non-causal components (Pedhazer 1982). Causal components can be direct or indirect effects (mediated through another variable); non-causal components can be unanalyzed correlation (due to an unknown cause or where data was not available) or spurious correlation (due to a common causal variable). The total effect (effect coefficient) of one

variable on another is the sum of the direct and indirect causal effects. (See Pedhazur 1982 and Schemske and Horvitz 1988 for complete discussions of the decomposition of correlations in path analysis).

We used path analysis to estimate the strengths and relative importance of causal relationships in a conceptual model we developed (Fig. 2). We included feces, nitrogen fixation, and litter accumulation in our model because all were affected by geese, but did not include variables such as root biomass, litter C:N ratios, or soil temperature, as they were not different between grazed and exclosed plots (see Results). We assumed feces, nitrogen fixation, and litter accumulation were correlated rather than causally linked. Small organic molecules released from feces, cyanobacterial mats, and litter could increase organic nitrogen pool sizes; however, we assumed only litter, which potentially stores much more nitrogen than feces or bacterial mats, could affect soil C:N ratios. Soil C:N ratios are often inversely related to net nitrogen mineralization (Ruess and McNaughton 1987, Frank et al. 1994). We assumed that the size of the organic nitrogen pool could affect organic nitrogen uptake by microbes, which could in turn affect the rate of nitrogen mineralization. Finally, larger organic molecules in litter and feces may directly act as substrate for nitrogen mineralization.

Except for litter accumulation (August 1997) and nitrogen fixation (August 1996), all variables were measured in May 1997 in the sedge meadow community, when we found significant treatment differences in net nitrogen mineralization (see Results). We assumed that August 1997 litter accumulation was inversely related to litter trampled into soil in the spring of 1997. We used August 1996 nitrogen fixation in the model,

assuming nitrogen fixed during that fall would be released to soils following decomposition of cyanobacterial mats over the winter and in the spring. Organic nitrogen production is labeled “microbial organic nitrogen uptake” in the model, as there was no net organic nitrogen production in May in buried bags, only net uptake into microbial biomass (negative values of net production; see Results). Soil C:N ratios at 5 cm depth are included in the model because there were significant differences between grazed and exclosed plots at this depth (see Results).

We ran multiple regressions in PROC GLM (SAS v.8) to obtain standardized regression coefficients (path coefficients) which give the magnitude and sign of direct causal effects (Mitchell 1993). Nitrogen mineralization rate, organic nitrogen pool size, and microbial organic nitrogen uptake were square root transformed to meet regression assumptions. We verified lack of collinearity in the regressions using the condition index (Philippi 1993). Because of low sample size ($n = 16$) in the regressions, we considered $P \leq 0.10$ to indicate significance. Unanalyzed causes of variation (U) are calculated as the square root of $1-R^2$ of the regression (Pedhazur 1982, Mitchell 1993). We calculated decomposition of correlations between variables in PROC CALIS (SAS v.8).

RESULTS

Net nitrogen mineralization rates

In the sedge meadow community, net nitrogen mineralization rates were twice as great in grazed plots compared to exclosed plots in May, although rates did not differ over the rest of the growing season, resulting in a month x treatment interaction (Fig. 3A,

Table 1). The total nitrogen mineralized over the growing season was 59% greater in grazed plots ($1.70 \pm 0.21 \text{ g N/m}^2$) than in exclosed ($1.07 \pm 0.18 \text{ g N/m}^2$; $F_{1,30} = 5.97$, $P = 0.02$). Mineralization rates in both types of plots decreased over the growing season (Fig. 3A). In contrast, in the herb meadow community, there was no treatment effect on net nitrogen mineralization (Fig. 4A, Table 1), or on the total nitrogen mineralized (grazed: $1.25 \pm 0.13 \text{ g N/m}^2$; exclosed: $1.32 \pm 0.15 \text{ g N/m}^2$; $F_{1,47} = 0.13$, $P = 0.72$). Net mineralization rates were much higher in June than in either May or July (Fig. 4A), due to a large increase in nitrification rates.

Although our ANOVA model assumed no transect x treatment interaction, one transect in the herb meadow community had extremely low mineralization rates compared to the other transects. Eliminating the anomalous transect from the analysis resulted in an estimate of 47% greater mineralization rates in grazed plots in May ($0.078 \pm 0.013 \text{ } \mu\text{g N} \cdot \text{g dwt}^{-1} \cdot \text{day}^{-1}$) compared to exclosed ($0.053 \pm 0.010 \text{ } \mu\text{g N} \cdot \text{g dwt}^{-1} \cdot \text{day}^{-1}$; $F_{1,31} = 3.53$, $P = 0.07$; ranks: $F_{1,31} = 4.56$, $P = 0.04$).

Extractable organic nitrogen

In the sedge meadow community, there was no overall effect of grazing on organic nitrogen pool size or net production rate (Fig. 3B and C, Table 1). However, in May, organic nitrogen pools were 20% larger in grazed plots ($F_{1,31} = 3.49$, $P = 0.07$; Fig. 3B). In the herb meadow community, there was no effect of grazing on either organic nitrogen pool size or on organic nitrogen net production (Fig. 4B and C, Table 1).

Microbial nitrogen

In the sedge meadow community, there were no differences in microbial nitrogen between grazed and exclosed plots throughout the summer (Fig. 3D, Table 1). In contrast, in the herb meadow community, microbial nitrogen showed an overall treatment effect (Fig. 4D, Table 1), due principally to the higher microbial nitrogen in grazed plots in July ($F_{1, 15} = 5.50$, $P = 0.03$). There was no correlation between microbial nitrogen and net nitrogen mineralization in the sedge meadow ($r = -0.03$, $P = 0.86$) or in the herb meadow ($r = 0.03$, $P = 0.84$).

Soil characteristics

Geese had little effect on microclimate in the sedge meadow community. Although soil temperature and moisture changed throughout the growing season, grazing did not affect these properties (Table 2). Similarly, there were no treatment effects on soil salinity or bulk density (Table 2). The higher pH in exclosed plots compared to grazed, although statistically significant, was slight, and probably not of biological significance (Table 2).

Soil C:N ratios at 10 cm (the depth of the buried bags) did not differ between grazed and exclosed plots in the sedge meadow (Table 2). However, at the 5 cm depth, C:N ratios showed an overall treatment effect (ranks: $F_{1, 23} = 4.39$, $P = 0.05$), and were significantly lower in grazed plots relative to ungrazed plots in both May ($F_{1, 31} = 4.48$, $P = 0.04$) and June ($F_{1, 31} = 5.35$, $P = 0.03$). In May, significantly higher soil nitrogen in grazed plots ($F_{1, 31} = 5.71$, $P = 0.02$) was responsible for the lower C:N ratios (Table 2).

Differences in soil nitrogen between treatments, although slight, translated into 4.7 g/m^2 more nitrogen in the top 5 cm of soil in grazed plots. In June, slightly lower soil carbon and higher soil nitrogen, neither statistically significant, resulted in lower C:N ratios in grazed plots (Table 2).

Geese had more effect on microclimate in the herb meadow community, although effects were minor. Soil temperatures at 3 cm depth were significantly greater in grazed plots, although only by $0.3 - 0.5 ^\circ\text{C}$ (Table 3). Bulk density was 6% greater on grazed compared to exclosed plots (Table 3). As in the sedge meadow, pH was slightly lower in grazed plots (Table 3). There were no treatment effects on soil moisture or salinity (Table 3). There was no effect of grazing on soil C:N ratios at 10 cm depth (Table 3). At 5 cm, grazed plots had slightly higher C:N ratios (Table 3).

Nitrogen fixation

We found the cyanobacterial nitrogen-fixing genera *Oscillatoria* and *Lyngbya* growing on salt marsh soils (Bold et al. 1987, Stal 1995). In August 1996 nitrogen fixation rates were 90 to 160% greater in grazed compared to exclosed plots for both the sedge meadow ($F_{1, 15} = 10.94$, $P = 0.005$; Fig. 5A) and herb meadow ($F_{1, 15} = 11.90$, $P = 0.004$; Fig. 5B). In May 1997, there was no effect of grazing on nitrogen fixation in the sedge meadow community ($F_{1, 31} = 0.003$, $P = 0.96$; Fig. 5A) or the herb meadow community ($F_{1, 30} = 0.06$, $P = 0.81$; Fig. 5B). In August 1997, rates of nitrogen fixation were 38% greater in grazed plots in the sedge meadow community, although this effect was marginally significant ($F_{1, 31} = 3.54$, $P = 0.07$; Fig. 5A). In the herb meadow

community in August of 1997, there was no treatment effect on fixation rates ($F_{1,47} = 0.96$, $P = 0.33$; Fig. 5B).

Plant carbon and nitrogen

In the sedge meadow community offtake plots sampled in May, there was no effect of grazing on plant C:N ratios in 1996 (*Carex*: $F_{1,3} = 0.11$, $P = 0.76$; *Triglochin*: $F_{1,3} = 0.09$, $P = 0.78$) or in 1997 (*Carex*: $F_{1,3} = 1.00$, $P = 0.39$; *Triglochin*: $F_{1,3} = 0.05$, $P = 0.84$). Similarly, there was no effect of grazing on C:N ratios in offtake plots in the herb meadow community in 1996 (*Triglochin*: $F_{1,17} = 0.79$, $P = 0.39$; *Plantago* shoots: $F_{1,4} = 0.25$, $P = 0.70$; *Plantago* roots: $F_{1,10} = 1.66$, $P = 0.23$; *Carex*: $F_{1,13} = 3.48$, $P = 0.08$) or in 1997 (*Triglochin*: $F_{1,17} = 0.57$, $P = 0.46$; *Plantago* shoots: $F_{1,8} = 0.61$, $P = 0.46$; *Plantago* roots: $F_{1,8} = 0.43$, $P = 0.53$; *Carex*: $F_{1,16} = 0.33$, $P = 0.58$).

In the sedge meadow community, there was no treatment effect on plant or litter C:N ratios on plots sampled in August of 1996 and 1997 after two and three years of fencing, respectively (Fig. 6A and B). In contrast, in the herb meadow community, *Potentilla* and *Plantago* shoots had lower C:N ratios in grazed plots in 1997, with *Potentilla* also showing this effect in 1996 (Fig. 6C and D). Lower C:N ratios in both species were due to significantly higher nitrogen levels (*Potentilla* 1996: $F_{1,51} = 15.21$, $P = 0.0003$; *Potentilla* 1997: $F_{1,55} = 9.63$, $P = 0.003$; *Plantago* 1997: $F_{1,33} = 6.96$, $P = 0.01$). In contrast, in 1996 *Triglochin* had higher C:N ratios in grazed areas, although there was no treatment effect in 1997 (Fig. 6C and D). Litter C:N ratios were also higher in grazed plots in 1997 (Fig. 6D).

Path analysis

The path diagram in Figure 7 and the regression equations in Table 4 give the magnitude, direction, and significance of direct effects in the path analysis. Litter accumulation had a negative effect on nitrogen mineralization rates by increasing soil C:N ratios and decreasing soil organic nitrogen pool size, but did not have a significant direct effect on mineralization. Nitrogen fixation had a positive effect on mineralization by increasing organic nitrogen pool size. Feces had no significant direct or indirect effects on nitrogen mineralization. The causal diagram explained 55% of the variation in nitrogen mineralization rates ($1 - \text{unanalyzed causes} = 1 - U$). Decompositions of correlations between variables are given in table 5. Litter accumulation had a much larger total effect (effect coefficient) on nitrogen mineralization than feces or nitrogen fixation.

DISCUSSION

Using the net rate of inorganic nitrogen production (net nitrogen mineralization) as an index of plant-available nitrogen (Haynes 1986b), we found that geese increased inorganic nitrogen availability to plants in the sedge meadow community, but did not affect inorganic nitrogen availability in the herb meadow. Net production rates probably estimate plant-available nitrogen better than pool sizes, as rapidly cycling small pools can potentially provide more nitrogen than slowly cycling large pools. Because many plants are able to take up amino acids present in organic nitrogen pools (Kielland 1994, Schimel and Chapin 1996), the net production of organic nitrogen can similarly be used as an

index of organic nitrogen availability to plants. Using this index, we found that geese did not affect organic nitrogen availability in either plant community.

Mechanisms affecting net nitrogen mineralization rates – sedge meadow community

Greater rates of net nitrogen mineralization found in grazed areas in the sedge meadow community cannot be explained by most established mechanisms through which animals alter nitrogen cycling (changes in litter quality or quantity, changes in root biomass, alteration of microclimate, fecal input). For example, changes in litter quality due to grazing can lead to increased (Sirotnak and Huntly 2000) or decreased (Pastor et al. 1993, Ritchie et al. 1998, Sirotnak and Huntly 2000) net nitrogen mineralization rates or nitrogen availability, but we found no difference in litter C:N ratios between grazed and exclosed plots. We also found no difference in belowground biomass between grazed and exclosed plots (Zacheis et al., *in press*). Reduction of root biomass through grazing may, over the long term, reduce microbial immobilization of nitrogen (Holland and Detling 1990, Holland et al. 1992).

We hypothesized that reductions in the thickness of the litter layer in grazed areas could alter soil moisture (House et al. 1984, Holland and Coleman 1987), temperature (Holland and Coleman 1987, Tian et al. 1997), or salinity (Bertness 1991), which have been shown to impact nitrogen mineralization rates (Singh et al. 1969, Haynes 1986a, Nadelhoffer et al. 1991, Binkley et al. 1994). However, there were no differences in these microclimate variables between grazed and exclosed plots.

Fecal input was so small in 1997 (1.8 feces/m^2 ; Zacheis et al., *in press*) that it was unlikely to affect mineralization rates. This was confirmed in the path analysis, where feces had no significant direct or indirect effects on nitrogen mineralization. We found a fecal pellet to average $0.366 \text{ g dry weight}$, with a total nitrogen content of 1.08% , based on feces collected from captive snow geese fed on vegetation from the sedge meadow. Nitrogen inputs from excreta in the sedge meadow plots in 1997 thus averaged 0.007 g N/m^2 ($1.8 \text{ feces/m}^2 * 0.366 \text{ g/feces} * 1.08\% \text{ N}$). If all nitrogen within feces were mineralized, it would account for only 1% of the additional 0.63 g N mineralized in grazed plots, clearly not constituting an important source of nitrogen. Fecal nitrogen inputs are naturally greater in years where grazing intensity in the marsh is higher. However, even with three fold higher grazing intensity, as was seen in 1996 (Zacheis et al., *in press*), feces would still constitute only a minor nitrogen source.

Nitrogen mineralization can be primed by the addition of uric acid or soluble nitrogen in fecal pellets, so that more nitrogen is mineralized from soil organic matter than would be mineralized without the amendment (Broadbent 1965, Yaacob and Blair 1980). Thus the difference in nitrogen mineralized between grazed and exclosed plots can be greater than the total amount of nitrogen added in feces. Organic residues, such as litter, may also prime mineralization (Broadbent and Nakashima 1974, Yaacob and Blair 1980, Haynes 1986a). In the sedge meadow community in 1997 the amount of nitrogen contained in litter was 530 times the amount of nitrogen in fecal material ($3.7 \text{ g/m}^2 = 282 \text{ g dry weight of peak biomass and litter in 1996} * 1.3 \% \text{ nitrogen in litter}$), with a similar C:N ratio (20 for feces and 25 for litter). It seems likely that if priming of soil organic

matter is occurring, it is through the much more massive input of organic material in litter, than through the minor fecal input. The relative importance of feces and litter to nitrogen mineralization are confirmed in the path analysis, where the total effect (effect coefficient) of litter on mineralization is much larger than that of feces (Table 5). In general, fecal and urinary inputs must be very large compared to litter inputs to increase nitrogen mineralization (Frank and McNaughton 1992, Frank et al. 1994, Frank and Groffman 1998), unless accompanied by changes in litter quality (McNaughton et al. 1988, Seagle et al. 1992, Hobbs 1996, Sirotinak and Huntly 2000) or root biomass (Holland and Detling 1990, Holland et al. 1992).

Litter production rates in the sedge meadow community were not affected by herbivory. Although we did not measure litterfall directly, we estimate it was similar between treatments, because both peak biomass and species composition did not differ between grazed and exclosed plots (Zacheis et al., *in press*). Therefore reduced litter production in grazed areas cannot be responsible for lower mineralization rates due to a lack of substrate available for decomposition (Pastor et al. 1984, McNaughton et al. 1988), as seen in other systems (Pastor et al. 1993, Biondini et al. 1998, van Wijnen et al. 1999).

Although litter production rates were not affected by herbivory, litter accumulation in 1997 in grazed areas was approximately 50% less than in exclosures (Zacheis et al., *in press*). We attribute the loss of litter in grazed plots to trampling by geese. Soils were covered with several centimeters of standing water in the spring, so

that trampling by geese could mix litter into the soil. The lack of litter on soil surfaces in the spring after the birds have departed was visually striking.

We suggest that decomposition of litter was greater in grazed plots because trampling mixed litter into the soil. The physical placement of the litter is important as incorporated litter is in more intimate contact with soil microbial biomass and decomposes more quickly (Douglas et al. 1980, House et al. 1984, Hendrix et al. 1986, Holland and Coleman 1987, Cogle et al. 1989, Dao 1998). Trampling fragments litter and decreases particle size, which also may speed decomposition (Handayanto et al. 1997). Faster decomposition means that less nitrogen is immobilized in litter and nitrogen may cycle through the ecosystem more quickly (House et al. 1984, McNaughton et al. 1988, Manley et al. 1995). In agricultural systems where organic residues are plowed under, there are, in general, higher rates of residue and organic matter decomposition (Brown and Dickey 1970, Douglas et al. 1980, House et al. 1984, Hendrix et al. 1986, Cogle et al. 1989, Dao 1998), higher rates of net nitrogen mineralization (Douglas et al. 1980, Goh and Haynes 1986, Hendrix et al. 1986, Holland and Coleman 1987), and greater standing crop nitrogen in plants (House et al. 1984, Goh and Haynes 1986, Hendrix et al. 1986) compared to systems where residues are left on soil surfaces.

Faster decomposition does not necessarily mean higher rates of net nitrogen mineralization, however, as in some cases soils amended with organic residues may show net microbial immobilization of nitrogen (Thomsen 1993, Franzluebbers et al. 1995, Mary et al. 1996). Whether net mineralization or immobilization occurs after organic material is mixed into soil depends on both substrate quality and time, as there is usually

a period of net immobilization of varying intensity and length followed by net mineralization (Bosatta and Berendse 1984, Haynes 1986a, Franzluebbers et al. 1995, Mary et al. 1996, Whitmore and Handayanto 1997). In general, the narrower the C:N ratio of litter, the faster nitrogen is mineralized from a substrate (Whitmore and Handayanto 1997), although other factors besides C:N ratios influence this rate (Haynes 1986a, Mary et al. 1996, Becker and Ladha 1997, Heal et al. 1997). Adding organic materials with C:N ratios of 25-30 (and sometimes greater) to soil commonly results in net mineralization, often without a period of net immobilization (Douglas et al. 1980, Haynes 1986a, van Vuuren and Berendse 1993, Mary et al. 1996, Whitmore and Handayanto 1997). The relatively low C:N ratio (25:1) of litter in the sedge meadow community indicates a capacity for rapid mineralization of this substrate following addition to the soil.

The path analysis corroborates that litter incorporation increased net nitrogen mineralization, through increasing organic nitrogen pool size and decreasing soil C:N ratios (Fig. 7). Litter accumulation is inversely related to litter input through trampling. Less accumulation (more trampling input) increased organic nitrogen pool size (Fig. 7), as small organic molecules from litter entered soil nitrogen pools. Less accumulation (more trampling input) also decreased soil C:N ratios (Fig. 7). Soil C:N ratios may decrease following substrate incorporation if much of the carbon in the substrate is respired off, with a larger proportion of the nitrogen remaining in the soil (Broadbent and Nakashima 1974, Ladd et al. 1983, Haynes 1986a, Holland and Coleman 1987).

Although there is often no effect of grazing on soil C:N ratio (Pastor et al. 1993, Biondini

et al. 1998, Frank and Groffman 1998), soils with very low levels of organic carbon, such as in Susitna Flats, are more likely to show a response to grazing (Manley et al. 1995).

Trampling also affected nitrogen mineralization through removal of the litter mat, improving the soil surface for cyanobacterial growth and nitrogen fixation. Nitrogen released from decomposing cyanobacterial mats formed in the fall of 1996 increased organic nitrogen pool size in the spring of 1997 (Fig. 7). This source of nitrogen for organic pools was as important as litter (compare effect coefficients of litter accumulation and nitrogen fixation on DON pool size in Table 5). However, nitrogen fixation was clearly secondary in importance to litter incorporation in affecting nitrogen mineralization (compare effect coefficients of litter and nitrogen fixation on nitrogen mineralization in Table 5).

Another effect of trampling that may lead to increased mineralization rates is a disturbance effect where soil aggregates are broken up, aeration is increased, organic matter is physically exposed to microbial communities, and soil temperatures may increase (Goh and Haynes 1986, Haynes 1986a, Dao 1998). Such a disturbance effect is probably minor in Susitna Flats, where only the top 1-2 cm of soil is disturbed by trampling. Trampling may also reduce nitrogen loss from the marsh by reducing nitrogen volatilization from standing dead and litter (Woodmansee 1978, Floate 1981, Schimel et al. 1986, Bauer et al. 1987), and by lowering tidal export of litter.

Nitrogen mineralization – herb meadow community

In contrast to the sedge meadow community, there was no effect of grazing on the availability of either inorganic or organic nitrogen in the herb meadow community. Both soil moisture and use by geese were lower in the herb meadow than in the sedge meadow (Zacheis et al., *in press*), and there was little standing water on the soil in April when birds were present. This combination of factors may have significantly reduced litter incorporation into soil by trampling, with the result that use by geese did not affect nitrogen cycling in this community in 1997.

Microbial nitrogen

In Susitna Flats, nitrogen mineralization rates and microbial biomass nitrogen were not correlated and, in addition, were not affected by grazing in a similar manner. For example, mineralization rates were greater in grazed areas in the sedge meadow in May, but microbial biomass was not different between grazed and exclosed plots. In the herb meadow, grazing did not affect mineralization rates in July, but microbial biomass was greater in grazed plots. Other studies have found an effect of herbivory on nitrogen mineralization without a corresponding change in microbial biomass (Pastor et al. 1988, Tracy and Frank 1998), an effect of herbivory on microbial biomass without a change in mineralization rates (Pastor et al. 1988), or a lack of correlation between microbial nitrogen and mineralization rates (Ruess and Seagle 1994). The lack of a close link between mineralization rates and microbial biomass suggests that mineralization rates

may be related to microbial activity as opposed to the amount of microbial biomass (Tracy and Frank 1998).

Effects of grazing on plant nitrogen content and C:N ratios

Increased nitrogen mineralization in grazed areas in the sedge meadow did not result in greater tissue nitrogen concentrations in plants in grazed areas, either in the one-year offtake plots sampled in May, or in the three-year plots sampled in August. The dominant species *Triglochin* and *Carex* do not appear to increase shoot nitrogen in response to increased nitrogen availability. This was verified in a separate fertilization experiment, where neither species showed increased shoot nitrogen concentration following addition of 10 g N/m² slow release fertilizer (A. Zacheis, *unpublished data*).

In contrast, in the herb meadow community, *Potentilla* and *Plantago* had lower C:N ratios and higher shoot nitrogen concentration in grazed plots compared to plots exclosed for three years. Because mineralization rates did not show a grazing effect in this community, the mechanism responsible for higher shoot nitrogen in these species is unclear. Mineralization rates could have been greater in grazed areas in previous years when soils were wetter and there was greater use of the community by geese (Zacheis et al., *in press*), with plants subsequently storing nitrogenous compounds over winter. Alternatively, higher shoot nitrogen could be due to greater nitrogen uptake per unit root biomass following grazing (Ruess et al. 1983, Jaramillo and Detling 1988, Polley and Detling 1989) or decreased competition for nitrogen with conspecifics in grazed plots

(these species had lower biomass in grazed plots compared to exclosed; Zacheis et al., *in press*).

Litter C:N ratios in the herb meadow were significantly greater in grazed compared to exclosed plots in 1997. This is probably due to both differences in relative species abundance between grazed and exclosed plots (more *Carex* and less *Plantago* and *Potentilla* in grazed plots; Zacheis et al., *in press*) and treatment differences in shoot C:N ratios within species. The long-term effect of higher litter C:N ratios in grazed plots may be a decrease in net mineralization rates (Pastor et al. 1993, Ritchie et al. 1998, Sirotinak and Huntly 2000).

Effects of grazing on the quality of goose diets

Grazing by geese in Susitna Flats did not result in a higher quality diet for geese because the effects of grazing on shoot nitrogen did not coincide with the period geese were in the marsh. Vegetation re-grown following grazing may have higher shoot nitrogen than ungrazed vegetation (Ydenberg and Prins 1981, Hik et al. 1991, Fox et al. 1998). As shoot nitrogen is an important determinant of food preference in geese (Sedinger and Raveling 1984, Gauthier and Bédard 1990) diet quality may thus be enhanced by grazing. In Susitna Flats, there were no effects of grazing on plant nitrogen concentration in the offtake plots, sampled within two weeks after the birds left the marsh, indicating that the residence time of the geese was too short for effects of grazing on forage quality to appear. As geese do not return to Susitna Flats in the autumn, they could not benefit from the higher shoot nitrogen of *Plantago* and *Potentilla* in grazed

areas in August. However, if these plants were able to store additional nitrogen over winter, they could potentially have higher root or shoot nitrogen concentrations in grazed areas the following spring. We are not able to address this hypothesis, as we did not sample three-year exclosures in the spring. This could potentially impact snow goose diets, as they feed on *Plantago* roots, although not on *Plantago* or *Potentilla* shoots (Zacheis et al., *in press*). Canada geese do not feed on either *Plantago* or *Potentilla* (Zacheis et al., *in press*).

CONCLUSIONS

Grazed areas in the sedge meadow community had higher rates of net nitrogen mineralization due to trampling by geese. Litter trampled into soil increased organic nitrogen pool size and decreased soil C:N ratio, and led to greater rates of nitrogen mineralization. Trampling also increased the extent of bare (non-littered) soil in the marsh, which facilitated the growth of nitrogen-fixing cyanobacteria. Nitrogen from cyanobacterial mats increased organic nitrogen pool size and again led to increased mineralization rates. In the herb meadow community, soils were probably too dry and goose use too light for trampling to have a large effect.

In the sedge meadow, trampling increased substrate availability to microbial communities and nitrogen availability to plant communities but did not result in higher quality forage for herbivores. In the herb meadow, trampling did not affect nitrogen cycling; however, *Plantago* and *Potentilla* had higher shoot nitrogen concentrations in grazed areas through an unknown mechanism. Higher nitrogen concentration in these

species in grazed areas was not coincident with goose staging, but could potentially impact snow goose diets if higher nitrogen levels could carry over into the next spring.

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LITERATURE CITED

- Bauer, A., C. V. Cole, and A. L. Black. 1987. Soil property comparisons in virgin grasslands between grazed and nongrazed management systems. *Soil Science Society of America Journal* **51**:176-182.
- Bazely, D. R., and R. L. Jefferies. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. *Journal of Applied Ecology* **22**:693-703.
- Bazely, D. R., and R. L. Jefferies. 1986. Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *Journal of Ecology* **74**:693-706.
- Bazely, D. R., and R. L. Jefferies. 1989. Lesser snow geese and the nitrogen economy of a grazed salt marsh. *Journal of Ecology* **77**:24-34.
- Becker, M., and J. K. Ladha. 1997. Synchronizing residue N mineralization with rice N demand in flooded conditions. Pages 231-238 *in* G. Cadish and K.E. Giller, editors. *Driven by nature: plant litter quality and decomposition*. CAB International, Wallingford, UK.
- Ben-David, M., R. T. Bowyer, L. K. Duffy, D. D. Roby, and D. M. Schell. 1998. Social behavior and ecosystem processes: river otter latrines and nutrient dynamics of terrestrial vegetation. *Ecology* **79**:2567-2571.
- Bertness, M. D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* **72**:125-137.

- Binkley, D., R. Stottlemeyer, F. Suarez, and J. Cortina. 1994. Soil nitrogen availability in some arctic ecosystems in northwest Alaska: Responses to temperature and moisture. *Écoscience* **1**:64-70.
- Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. *Ecological Applications* **8**:469-479.
- Bold, H. C., C. J. Alexopoulos, and T. Delevoryas. 1987. Morphology of plants and fungi. Fifth edition. Harper and Row, New York, New York, USA.
- Bosatta, E., and F. Berendse. 1984. Energy or nutrient regulation of decomposition: implications for the mineralization-immobilization response to perturbations. *Soil Biology and Biochemistry* **16**:63-67.
- Broadbent, F. E. 1965. Effects of fertilizer nitrogen on the release of soil nitrogen. *Soil Science Society Proceedings* **29**:692-695.
- Broadbent, F. E., and T. Nakashima. 1974. Mineralization of carbon and nitrogen in soil amended with carbon-13 and nitrogen-15 labeled plant material. *Soil Science Society of America Proceedings* **38**:313-315.
- Brookes, P. C., A. Landman, G. Pruden, and D. S. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry* **17**:837-842.
- Brown, P. L., and D. D. Dickey. 1970. Losses of wheat straw residue under simulated field conditions. *Soil Science Society of America Proceedings* **34**:118-121.

- Butler, W. I., Jr., and R. E. Gill. 1987. Spring 1986 aerial surveys of geese and swans staging in Upper Cook Inlet. U.S. Fish and Wildlife Service, Anchorage, Alaska, USA.
- Cogle, A. L., P. G. Saffigna, and W. M. Strong. 1989. Carbon transformations during wheat straw decomposition. *Soil Biology and Biochemistry* **21**:367-372.
- Conover, W. J. 1980. Practical nonparametric statistics. Second edition. John Wiley and Sons, New York, New York, USA.
- Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* **56**:1-9.
- Dao, T. H. 1998. Tillage and crop residue effects on carbon dioxide evolution and carbon storage in a Paleustoll. *Soil Science Society of America Journal* **62**:250-256.
- Day, T. A., and J. K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* **71**:180-188.
- Dormaar, J. F., S. Smoliak, and W. D. Willms. 1990. Distribution of nitrogen fractions in grazed and ungrazed fescue grassland Ah horizons. *Journal of Range Management* **43**:6-9.
- Douglas, C. L., Jr., R. R. Allmaras, P. E. Rasmussen, R. E. Ramig, and N. C. Roager, Jr. 1980. Wheat straw composition and placement effects on decomposition in

- dryland agriculture of the Pacific Northwest. Soil Science Society of America Journal **44**:833-837.
- Eno, C. F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Science Society of America Proceedings **35**:277-279.
- Floate, M. J. S. 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. Pages 585-601 in F. E. Clark and T. Roswall, editors. Terrestrial nitrogen cycles. Ecological Bulletin 33, Stockholm, Sweden.
- Fox, A. D., J. N. Kristiansen, D. A. Stroud, and H. Boyd. 1998. The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves. Oecologia **116**:154-159.
- Frank, D. A., and P. M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology **79**:2229-2241.
- Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry **26**:163-188.
- Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology **73**:2043-2058.
- Franzluebbers, A. J., F. M. Hons, and D. A. Zuberer. 1995. Tillage and crop effects on seasonal soil carbon and nitrogen dynamics. Soil Science Society of America Journal **59**:1618-1624.
- Gauthier, G., and J. Bédard. 1990. The role of phenolic compounds and nutrients in determining food preference in greater snow geese. Oecologia **84**:553-558.

- Goh, K. M., and R. J. Haynes. 1986. Nitrogen and agronomic practice. Pages 379-468 *in* R. J. Haynes, editor. Mineral nitrogen in the plant-soil system. Academic Press Inc., Orlando, Florida, USA.
- Handayanto, E., G. Cadish, and K. E. Giller. 1997. Regulating N mineralization from plant residues by manipulation of quality. Pages 175-185 *in* G. Cadish and K. E. Giller, editors. Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, UK.
- Hardy, R. W. F., R. D. Holsten, E. K. Jackson, and R. C. Burns. 1968. The acetylene-ethylene assay for N₂ fixation: laboratory and field evaluation. *Plant Physiology* **43**:1185-1207.
- Haynes, R. J. 1986a. The decomposition process: mineralization, immobilization, humus formation, and degradation. Pages 52-126 *in* R. J. Haynes, editor. Mineral nitrogen in the plant-soil system. Academic Press Inc., Orlando, Florida, USA.
- Haynes, R. J. 1986b. Origin, distribution, and cycling of nitrogen in terrestrial ecosystems. Pages 1-51 *in* R. J. Haynes, editor. Mineral nitrogen in the plant-soil system. Academic Press Inc., Orlando, Florida, USA.
- Heal, O. W., J. M. Anderson, and M. J. Swift. 1997. Plant litter quality and decomposition: an historical overview. Pages 3-30 *in* G. Cadish and K.E. Giller, editors. Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, UK.

- Hendrix, P. F., R. W. Parmelee, D. A. Crossley, Jr., D. C. Coleman, E. P. Odum, and P. M. Groffman. 1986. Detritus food webs in conventional and no-tillage agroecosystems. *BioScience* **36**:374-380.
- Hik, D. S., H. A. Sadul, and R. L. Jefferies. 1991. Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. *Journal of Ecology* **79**:715-730.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* **60**:695-713.
- Holland, E. A., and D. C. Coleman. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* **68**:425-433.
- Holland, E. A., and J. K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology* **71**:1040-1049.
- Holland, E. A., W. J. Parton, J. K. Detling, and D. L. Coppock. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *American Naturalist* **140**:685-706.
- House, G. J., B. R. Stinner, D. A. Crossley, Jr., E. P. Odum, and G. W. Langdale. 1984. Nitrogen cycling in conventional and no-tillage agroecosystems in the Southern Piedmont. *Journal of Soil and Water Conservation* **39**:194-200.
- Hultén, E. 1968. *Flora of Alaska and neighboring territories*. Stanford University Press, Stanford, California, USA.

- Hupp, J. W., A. B. Zacheis, R. M. Anthony, D. G. Robertson, W. P. Erickson, and K.C. Palacios. *In press*. Snow cover and snow goose distribution during spring migration. *Wildlife Biology*.
- Jaramillo, V. J., and J. K. Detling. 1988. Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* **69**:1599-1608.
- Johnson, R. A., and D. W. Wichern. 1992. *Applied multivariate statistical analysis*. Third edition. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.
- Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology* **75**:2373-2383.
- Ladd, J. N., R. B. Jackson, M. Amato, and J. H. A. Butler. 1983. Decomposition of plant material in Australian soils. I The effect of quantity added on decomposition and on residual microbial biomass. *Australian Journal of Soil Research* **21**:563-570.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. SAS Institute Inc., Cary, North Carolina, USA.
- Manley, J. T., G. E. Schuman, J. D. Reeder, and R. H. Hart. 1995. Rangeland soil carbon and nitrogen responses to grazing. *Journal of Soil and Water Conservation* **50**:294-298.
- Mary, B., S. Recous, D. Darwis, and D. Robin. 1996. Interactions between decomposition of plant residues and nitrogen cycling in soil. *Plant and Soil* **181**:71-82.

- McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* **278**:1798-1800.
- McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *BioScience* **38**:794-800.
- Mitchell, R. J. 1993. Path analysis: pollination. Pages 211-231 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and J. A. Laundre. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* **72**:242-253.
- Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models. Third edition. Irwin, Homewood, Illinois, USA.
- Newman, J. A., J. Bergelson, and A. Grafen. 1997. Blocking factors and hypothesis tests in ecology: is your statistics text wrong? *Ecology* **78**:1312-1320.
- Pastor, J., J. D. Aber, C. A. McClaugherty, and J. M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* **65**:256-268.
- Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* **74**:467-480.
- Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. *BioScience* **38**:770-777.

- Pedhazur, E. J. 1982. Multiple regression in behavioral research. Second edition. Holt, Rinehart and Winston, New York, New York, USA.
- Philippi, T. E. 1993. Multiple regression: herbivory. Pages 183-210 *in* S.M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- Polley, H. W., and J. K. Detling. 1989. Defoliation, nitrogen, and competition: effects on plant growth and nitrogen nutrition. *Ecology* **70**:721-727.
- Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* **79**:165-177.
- Ruess, R. W. 1987. The role of large herbivores in nutrient cycling of tropical savannas. Pages 67-91 *in* B. H. Walker, editor. Determinants of tropical savannas. IRL Press Limited, Oxford, UK.
- Ruess, R. W., R. L. Hendrick, and J. P. Bryant. 1998. Regulation of fine root dynamics by mammalian browsers in early successional Alaskan taiga forests. *Ecology* **79**:2706-2720.
- Ruess, R. W., and S. J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos* **49**:101-110.
- Ruess, R. W., S. J. McNaughton, and M. B. Coughenour. 1983. The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an east african sedge. *Oecologia* **59**:253-261.

- Ruess, R. W., and S. W. Seagle. 1994. Landscape pattern in soil microbial processes in the Serengeti National Park, Tanzania. *Ecology* **75**:892-904.
- Schemske, D. W., and C. C. Horvitz. 1988. Plant-animal interactions and fruit production in a neotropical herb: a path analysis. *Ecology* **69**:1128-1137.
- Schimel, D. S., W. J. Parton, F. J. Adamsen, R. G. Woodmansee, R. L. Senft, and M. A. Stillwell. 1986. The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. *Biogeochemistry* **2**:39-52.
- Schimel, J. P., and F. S. Chapin, III. 1996. Tundra plant uptake of amino acid and NH_4^+ nitrogen in situ: plants compete well for amino acid N. *Ecology* **77**:2142-2147.
- Seagle, S. W., S. J. McNaughton, and R. W. Ruess. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. *Ecology* **73**:1105-1123.
- Sedinger, J. S., and D. G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. *Auk* **101**:295-306.
- Singh, B. R., A. S. Agarwal, and Y. Kanehiro. 1969. Effect of chloride salts on ammonium nitrogen release in two Hawaiian soils. *Soil Science Society of America Proceedings* **33**:557-560.
- Sirotnak, J. M., and N. J. Huntly. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* **81**:78-87.
- Stal, L. J. 1995. Physiological ecology of cyanobacteria in microbial mats and other communities. *New Phytologist* **131**:1-32.

- Tardiff, S. E., and J. A. Stanford. 1998. Grizzly bear digging: effect on subalpine meadow plants in relation to mineral nitrogen availability. *Ecology* **79**:2219-2228.
- Thomas, R. J., K. A. B. Logan, A. D. Ironside, and G. R. Bolton. 1988. Transformations and fate of sheep urine-N applied to an upland U.K. pasture at different times during the growing season. *Plant and Soil* **107**:173-181.
- Thomas, R. J., K. A. B. Logan, A. D. Ironside, and G. R. Bolton. 1990. The effects of grazing with and without excretal returns on the accumulation of nitrogen by ryegrass in a continuously grazed upland sward. *Grass and Forage Science* **45**:65-75.
- Thomas, R. J., K. A. B. Logan, A. D. Ironside, and J. A. Milne. 1986. Fate of sheep urine-N applied to an upland grass sward. *Plant and Soil* **91**:425-427.
- Thomsen, I. K. 1993. Turnover of ^{15}N -straw and NH_4NO_3 in a sandy loam soil: effects of straw disposal and N fertilization. *Soil Biology and Biochemistry* **25**:1561-1566.
- Tian, G., L. Brussaard, B. T. Kang, and M. J. Swift. 1997. Soil fauna-mediated decomposition of plant residues under constrained environmental and residue quality conditions. Pages 125-134 in G. Cadish and K. E. Giller, editors. *Driven by nature: plant litter quality and decomposition*. CAB International, Wallingford, UK.
- Tracy, B. F., and D. A. Frank. 1998. Herbivore influence on soil microbial biomass and nitrogen mineralization in a northern grassland ecosystem: Yellowstone National Park. *Oecologia* **114**:556-562.

- van Vuuren, M. M. I., and F. Berendse. 1993. Changes in soil organic matter and net nitrogen mineralization in heathland soils, after removal, addition or replacement of litter from *Erica tetralix* or *Molina caerulea*. *Biology and Fertility of Soils* **15**:268-274.
- van Wijnen, H. J., R. van der Wal, and J. P. Bakker. 1999. The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. *Oecologia* **118**:225-231.
- Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbance. *BioScience* **38**:778-785.
- Whitmore, A. P., and E. Handayanto. 1997. Simulating the mineralization of N from crop residues in relation to residue quality. Pages 337-348 in G. Cadish and K. E. Giller, editors. *Driven by nature: plant litter quality and decomposition*. CAB International, Wallingford, UK.
- Woodmansee, R. G. 1978. Additions and losses of nitrogen in grassland ecosystems. *BioScience* **28**:448-453.
- Yaacob, O., and G. J. Blair. 1980. Mineralization of ^{15}N -labelled legume residues in soils with different nitrogen contents and its uptake by Rhodes grass. *Plant and Soil* **57**:237-248.
- Ydenberg, R. C., and H. H. Th. Prins. 1981. Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology* **18**:443-453.

- Youngner, V. B. 1972. Physiology of defoliation and regrowth. Pages 292-303 *in* V. B. Youngner and C. M. McKell, editors. The biology and utilization of grasses. Academic Press, New York, New York, USA.
- Zaady, E., P. M. Groffman, and M. Shachak. 1996. Release and consumption of nitrogen by snail feces in Negev Desert soils. *Biology and Fertility of Soils* **23**:399-404.
- Zacheis, A. B., J. W. Hupp, and R. W. Ruess. *In press*. Effects of migratory geese on plant communities of an Alaskan salt marsh. *Journal of Ecology*.
- Zar, J. H. 1996. Biostatistical analysis. Third edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

TABLE 2.1. Results from repeated measures MANOVA analyses on the effects of grazing on soil nitrogen variables, sedge meadow and herb meadow communities, Susitna Flats, Alaska. Treatment effect compares grazed and exclosed plots; month effect compares May, June, and July 1997 samples. § $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

		Sedge meadow	Herb meadow
Net N mineralization	Treatment	$F_{1,30} = 5.82^*$	$F_{1,47} = 0.31$
	Month	$F_{2,29} = 14.12^{***}$	$F_{2,46} = 105.84^{***}$
	Month x Treatment	$F_{2,29} = 3.89^*$	$F_{2,46} = 1.64$
Organic N pool size	Treatment	$F_{1,30} = 1.76$	$F_{1,31} = 1.50$
	Month	$F_{2,29} = 22.42^{***}$	$F_{2,30} = 38.95^{***}$
	Month x Treatment	$F_{2,29} = 2.24$	$F_{2,30} = 0.15$
Organic N net production	Treatment	$F_{1,30} = 2.52$	$F_{1,31} = 0.18$
	Month	$F_{2,29} = 7.88^{**}$	$F_{2,30} = 9.13^{***}$
	Month x Treatment	$F_{2,29} = 1.54$	$F_{2,30} = 0.15$
Microbial N	Treatment	$F_{1,14} = 0.00$	$F_{1,15} = 4.46^*$
	Month	$F_{2,13} = 3.02§$	$F_{2,14} = 8.51^{**}$
	Month x Treatment	$F_{2,13} = 0.16$	$F_{2,14} = 1.27$

TABLE 2.2. Soil properties on grazed and exclosed plots in the sedge meadow community, Susitna Flats, Alaska, 1997. Values are means \pm 1 SE. *F*-values are from repeated measures MANOVA or univariate ANOVA analyses examining treatment (grazed/exclosed) and month effects. § $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Soil property	Month	Grazed	Exclosed	<i>F</i> -values
Soil temperature °C	May	10.65 \pm 0.23	10.58 \pm 0.20	Treatment: $F_{1,4} = 0.00$
	June	17.31 \pm 0.13	17.08 \pm 0.12	Month: $F_{3,12} = 209.78^{***}$
	July	17.47 \pm 0.08	17.65 \pm 0.07	Month x Treat: $F_{3,12} = 0.67$
	August	16.20 \pm 0.07	16.13 \pm 0.06	
Soil moisture %	May	38.49 \pm 0.59	38.20 \pm 0.42	Treatment: $F_{1,31} = 0.03$
	June	32.66 \pm 0.45	33.12 \pm 0.44	Month: $F_{2,30} = 207.98^{***}$
	July	35.85 \pm 0.54	35.90 \pm 0.55	Month x Treat: $F_{2,30} = 0.97$
Soil salinity ‰	May	14.89 \pm 0.75	14.13 \pm 0.76	Treatment: $F_{1,31} = 1.74$
	June	15.06 \pm 1.20	13.78 \pm 1.18	Month: $F_{1,31} = 0.02$ Month x Treat: $F_{1,31} = 0.18$

Soil pH	May	7.25 ± 0.04
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Bulk density g/cm ³	May	1.11 ± 0.02
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Total Soil C and N - 10 cm depth

% C	May	1.49 ± 0.09
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June	1.32 ± 0.07
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July	1.30 ± 0.05
------	-----------------

% N	May	0.106 ± 0.006
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June	0.092 ± 0.005
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July	0.107 ± 0.005
------	-------------------

C:N ratio	May	14.04 ± 0.27
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June	14.36 ± 0.22
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July	12.38 ± 0.48
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7.33 ± 0.04	Treatment: $F_{1, 31} = 4.82^*$
1.11 ± 0.02	Treatment: $F_{1, 31} = 0.00$
1.34 ± 0.08	Treatment: $F_{1, 15} = 1.00$
1.28 ± 0.07	Month: $F_{2, 14} = 1.52$
1.34 ± 0.05	Month x Treat: $F_{2, 14} = 0.90$
0.095 ± 0.004	Treatment: $F_{1, 15} = 2.26$
0.089 ± 0.003	Month: $F_{2, 14} = 29.75^{***}$
0.105 ± 0.005	Month x Treat: $F_{2, 14} = 0.65$
14.15 ± 0.30	Treatment: $F_{1, 15} = 1.04$
14.39 ± 0.22	Month: $F_{2, 14} = 21.32^{***}$
12.87 ± 0.41	Month x Treat: $F_{2, 14} = 0.37$

Total Soil C and N - 5 cm depth

% C	May	1.31 ± 0.04
	June	1.34 ± 0.04

% N	May	0.112 ± 0.004
	June	0.101 ± 0.003

C:N ratio	May	11.90 ± 0.31
	June	13.26 ± 0.25

1.29 ± 0.04

Treatment: $F_{1,23} = 0.01$

1.38 ± 0.05

Month: $F_{1,23} = 3.71§$

Month x Treat: $F_{1,23} = 1.02$

0.104 ± 0.003

Treatment: $F_{1,23} = 3.09§$

0.097 ± 0.002

Month: $F_{1,23} = 10.08^{**}$

Month x Treat: $F_{1,23} = 0.30$

12.38 ± 0.23

Treatment: $F_{1,23} = 3.00§$

14.19 ± 0.34

Month: $F_{1,23} = 42.14^{***}$

Month x Treat: $F_{1,23} = 0.86$

TABLE 2.3. Soil properties on grazed and exclosed plots in the herb meadow community, Susitna Flats, Alaska, 1997.

Values are means \pm 1 SE. *F*-values are from repeated measures MANOVA or univariate ANOVA analyses examining treatment (grazed/exclosed) and month effects. § $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Soil property	Month	Grazed	Exclosed	<i>F</i> -values
Soil temperature °C	May	10.84 \pm 0.13	10.48 \pm 0.11	Treatment: $F_{1,8} = 6.13^*$
	June	16.25 \pm 0.11	15.77 \pm 0.09	Month: $F_{3,16} = 567.56^{***}$
	July	17.88 \pm 0.06	17.42 \pm 0.05	Month x Treat: $F_{3,16} = 0.06$
	August	15.95 \pm 0.06	15.50 \pm 0.05	
Soil moisture %	May	33.61 \pm 0.59	33.68 \pm 0.59	Treatment: $F_{1,47} = 0.02$
	June	26.40 \pm 0.54	26.66 \pm 0.51	Month: $F_{2,46} = 400.05^{***}$
	July	31.18 \pm 0.41	30.97 \pm 0.42	Month x Treat: $F_{2,46} = 0.81$
Soil salinity ‰	May	11.55 \pm 0.49	10.95 \pm 0.46	Treatment: $F_{1,47} = 2.48$
	June	12.60 \pm 0.56	12.08 \pm 0.39	Month: $F_{1,47} = 11.42^{**}$ Month x Treat: $F_{1,47} = 0.01$

Soil pH	May	7.33 ± 0.02
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Bulk density g/cm ³	May	1.36 ± 0.02
--------------------------------	-----	-----------------

Total Soil C and N - 10 cm depth

% C	May	1.65 ± 0.07
-----	-----	-----------------

June	1.31 ± 0.06
------	-----------------

July	1.43 ± 0.07
------	-----------------

% N	May	0.113 ± 0.004
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June	0.098 ± 0.003
------	-------------------

July	0.120 ± 0.007
------	-------------------

C:N ratio	May	14.67 ± 0.39
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June	13.49 ± 0.50
------	------------------

July	12.03 ± 0.31
------	------------------

7.38 ± 0.02	Treatment: $F_{1, 47} = 3.62§$
1.28 ± 0.03	Treatment: $F_{1, 28} = 4.45^*$
1.53 ± 0.07	Treatment: $F_{1, 15} = 0.79$
1.33 ± 0.05	Month: $F_{2, 14} = 9.35^{**}$
1.37 ± 0.06	Month x Treat: $F_{2, 14} = 0.61$
0.105 ± 0.002	Treatment: $F_{1, 15} = 2.53$
0.094 ± 0.002	Month: $F_{2, 14} = 24.99^{***}$
0.116 ± 0.005	Month x Treat: $F_{2, 14} = 0.31$
14.64 ± 0.56	Treatment: $F_{1, 15} = 0.14$
14.06 ± 0.40	Month: $F_{2, 14} = 35.80^{***}$
11.89 ± 0.31	Month x Treat: $F_{2, 14} = 0.74$

Total Soil C and N - 5 cm depth

% C	May	1.09 ± 0.03
	June	1.15 ± 0.04
% N	May	0.083 ± 0.002
	June	0.078 ± 0.002
C:N ratio	May	13.23 ± 0.10
	June	14.77 ± 0.29

1.07 ± 0.03	Treatment: $F_{1,39} = 0.08$
1.13 ± 0.05	Month: $F_{1,39} = 4.78^*$
	Month x Treat: $F_{1,39} = 0.001$
0.083 ± 0.003	Treatment: $F_{1,39} = 0.05$
0.079 ± 0.003	Month: $F_{1,39} = 7.94^{**}$
	Month x Treat: $F_{1,39} = 0.38$
13.00 ± 0.11	Treatment: $F_{1,39} = 3.59§$
14.15 ± 0.22	Month: $F_{1,39} = 43.21^{***}$
	Month x Treat: $F_{1,39} = 0.90$

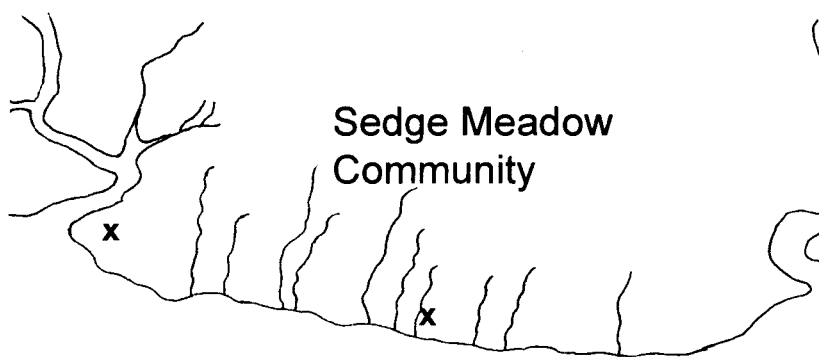
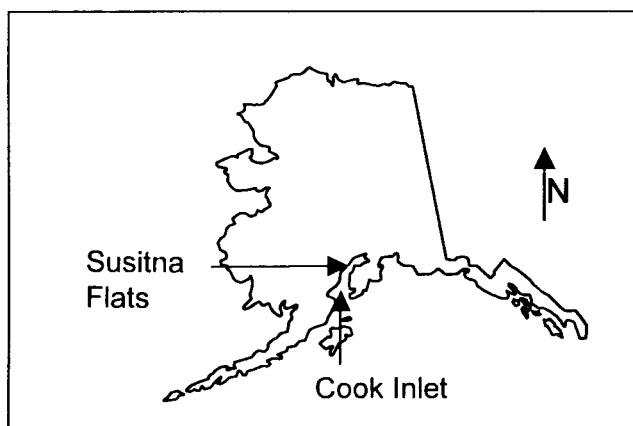
TABLE 2.4. Regression equations from the path analysis illustrated in Fig. 7. Path coefficients are standardized regression coefficients.

Dependent variable	Independent variables	R^2	Error d.f.	Path coefficient	t	P
Organic N pool size	Feces	0.46	12	-0.24	-0.92	0.37
	N fixation			0.48	2.05	0.06
	Litter accumulation			-0.46	-1.80	0.09
Organic N microbial uptake	Organic N pool size	0.77	14	0.88	6.78	0.0001
Soil C:N ratio	Litter accumulation	0.35	14	0.59	2.74	0.02
Net N mineralization	Organic N microbial uptake	0.79	11	0.49	3.14	0.01
	Soil C:N ratio			-0.39	-2.04	0.07
	Feces			0.22	1.22	0.25
	Litter accumulation			-0.15	-0.74	0.47

TABLE 2.5. Decomposition of correlated variables from the path analysis illustrated in Fig. 7. The effect coefficient is the sum of the direct and indirect effects, and represents the total causal effect of the second variable on the first.

Correlated variables		Direct effect	Indirect effect	Effect coefficient
Organic N pool size	Feces	-0.24	0	-0.24
	N fixation	0.48	0	0.48
	Litter accumulation	-0.46	0	-0.46
Organic N microbial uptake	Organic N pool size	0.88	0	-0.88
	Feces	0	0.21	0.21
	N fixation	0	-0.42	-0.42
	Litter accumulation	0	0.40	0.40
Soil C:N ratio	Litter accumulation	0.59	0	0.59
Net N mineralization	Organic N microbial uptake	0.49	0	0.49
	Soil C:N ratio	-0.39	0	-0.39
	Organic N pool size	0	0.43	0.43
	Feces	0.22	-0.10	0.12
	N fixation	0	0.21	0.21
	Litter accumulation	-0.15	-0.43	-0.57

FIG. 2.1. Location of study sites at Susitna Flats, Alaska. Transects where soil and plant sampling was done in 1997 are indicated with an **x**. Transects where additional plant and nitrogen fixation samples were collected in 1996 and 1997 are marked with an **o**.



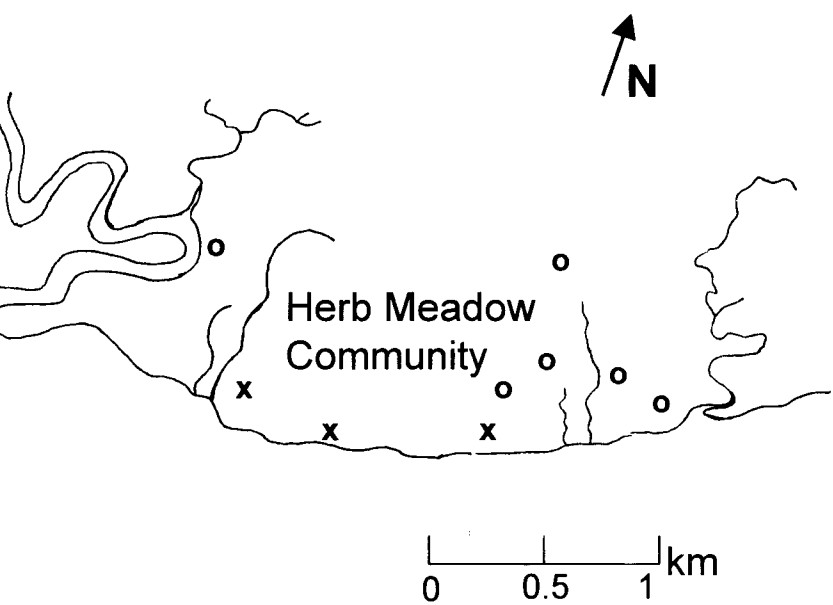
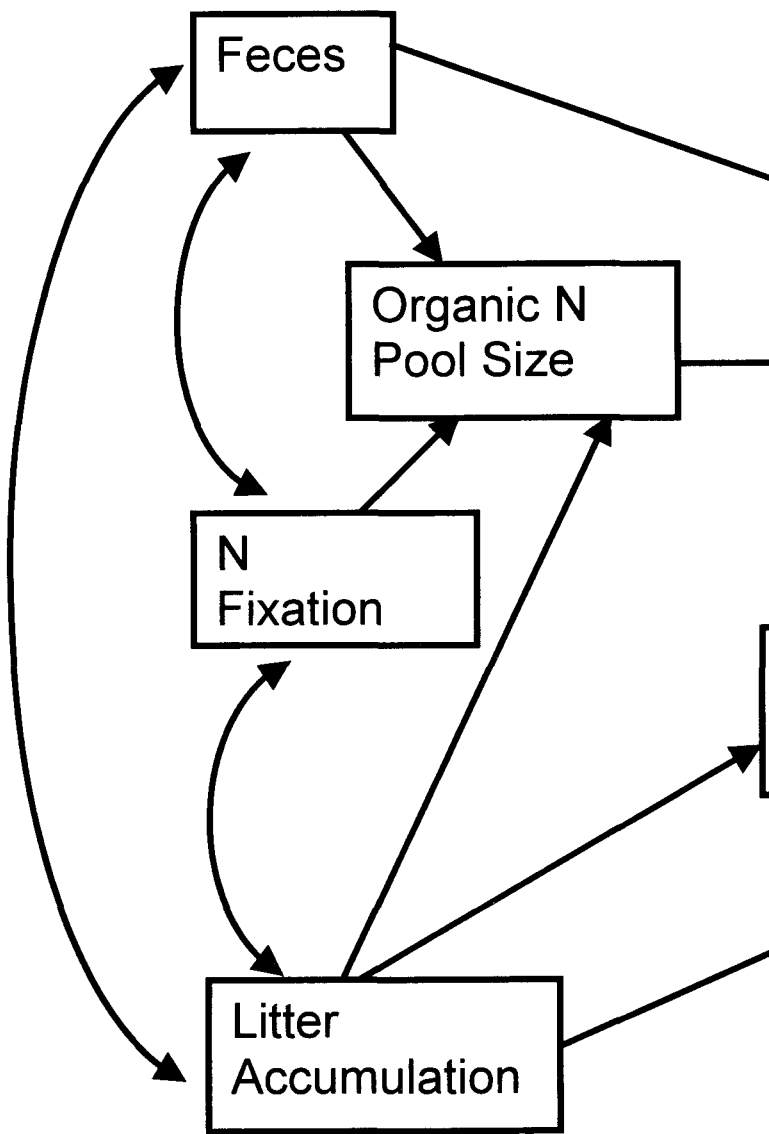


FIG. 2.2. Conceptual model of factors potentially responsible for differences in nitrogen mineralization between grazed and , exclosed plots, sedge meadow community, Susitna Flats, Alaska, May 1997. Double-headed arrows indicate correlations, while single-headed arrows indicate causal relationships.



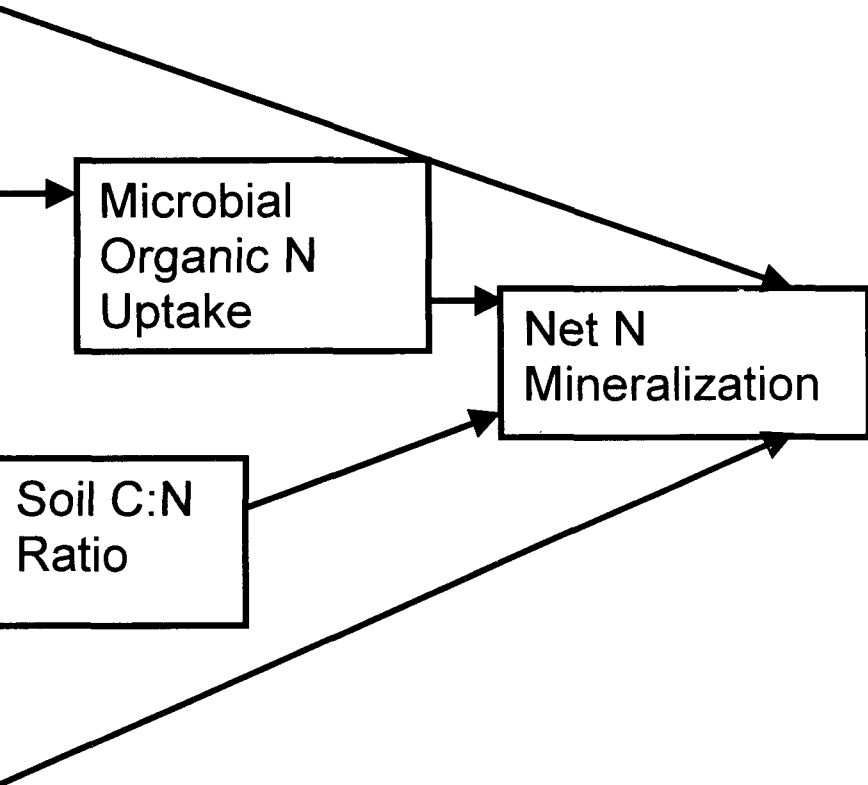
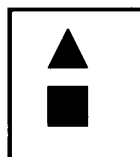
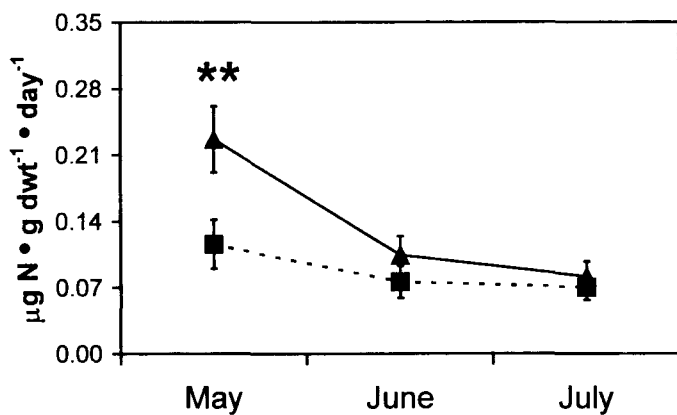


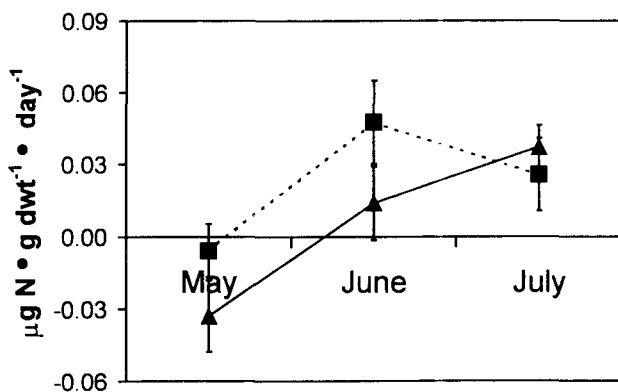
FIG. 2.3. Effects of geese on nitrogen dynamics, sedge meadow plant community, Susitna Flats, Alaska, 1997. Comparison of plots grazed by geese and those exclosed from geese for (A) net nitrogen mineralization, (B) extractable organic nitrogen pool size, (C) net organic nitrogen production, and (D) microbial nitrogen. Significant differences between grazed and exclosed plots are based on separate monthly ANOVAs, and are indicated by: ** $P \leq 0.01$.



A Net N Mineralization

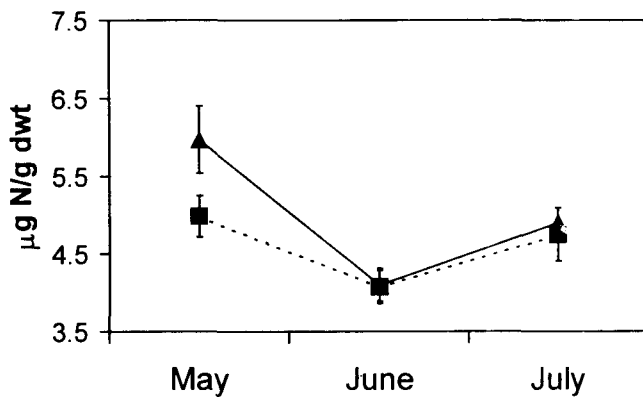


C Organic N Production



Grazed
Exclosed

B Organic N Pool Size



D Microbial N

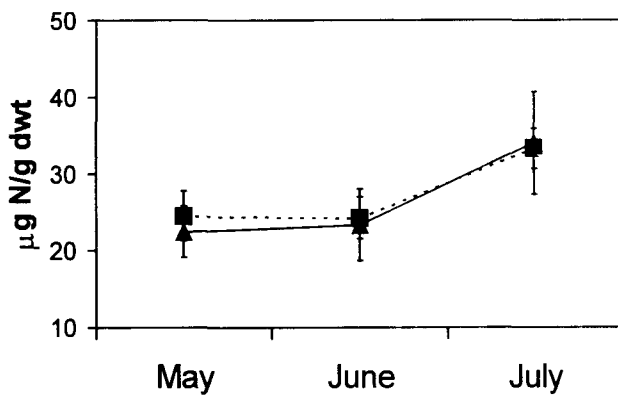
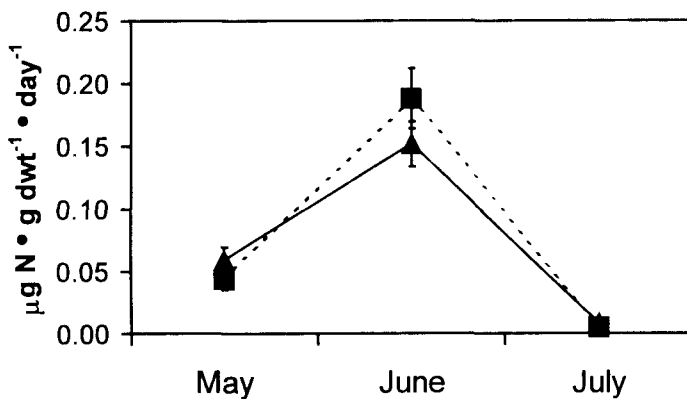


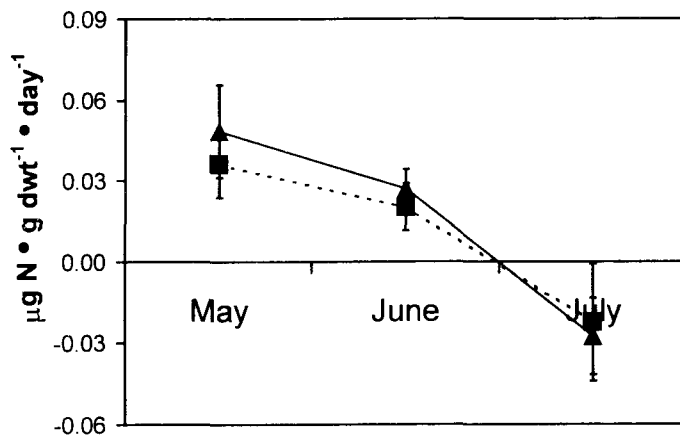
FIG. 2.4. Effects of geese on nitrogen dynamics, herb meadow plant community, Susitna Flats, Alaska, 1997. Comparison of plots grazed by geese and those exclosed from geese for (A) net nitrogen mineralization, (B) extractable organic nitrogen pool size, (C) net organic nitrogen production, and (D) microbial nitrogen. Significant differences between grazed and exclosed plots are based on separate monthly ANOVAs, and are indicated by: * $P \leq 0.05$.



A Net N Mineralization



C Organic N Production



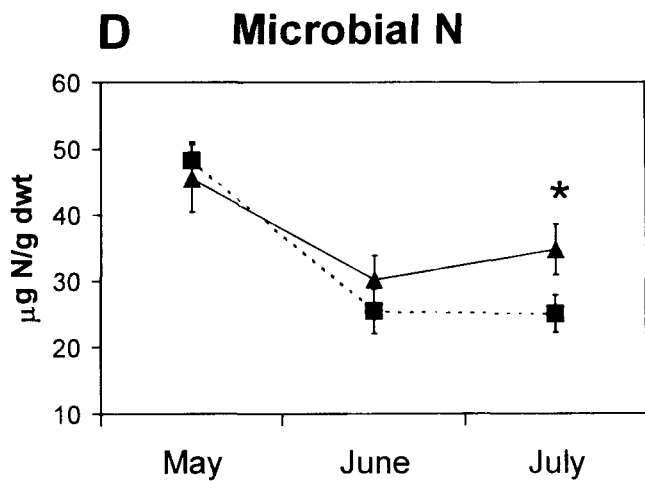
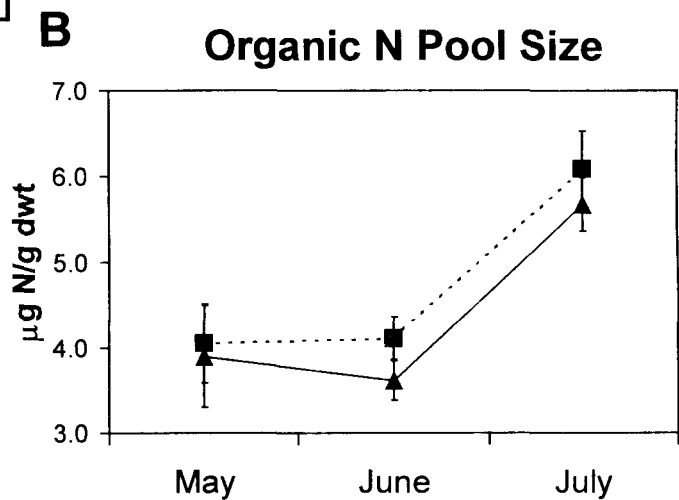


FIG. 2.5. Effects of geese on nitrogen fixation by cyanobacteria, sedge meadow and herb meadow plant communities, Susitna Flats, Alaska, 1996-97. Comparison of plots grazed by geese and those exclosed from geese in the (A) sedge meadow community and (B) herb meadow community. Significant differences between grazed and exclosed plots are indicated by: ** $P \leq 0.01$.

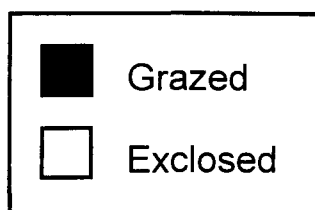
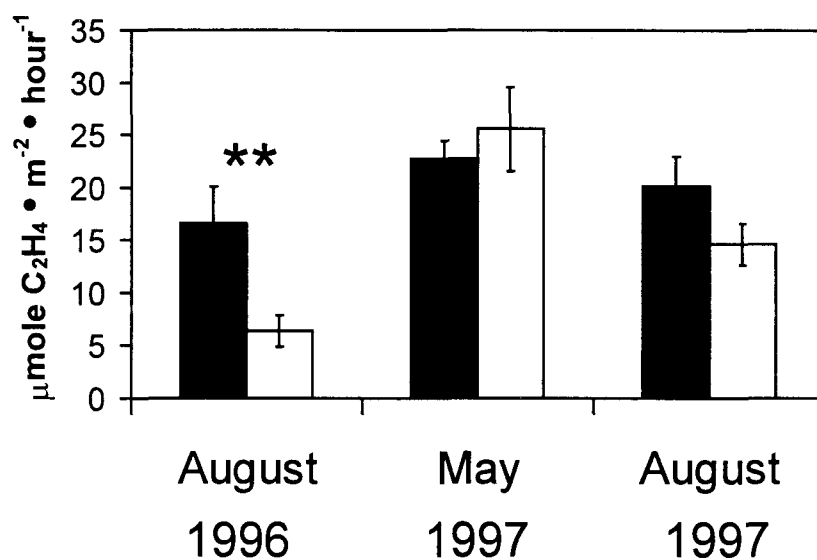
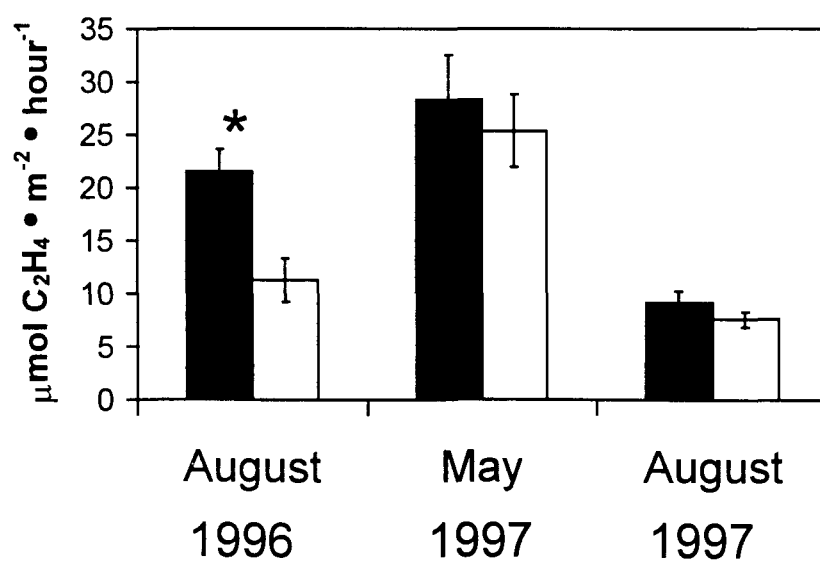
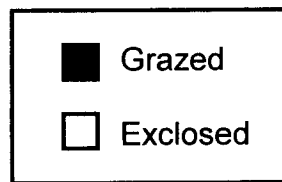
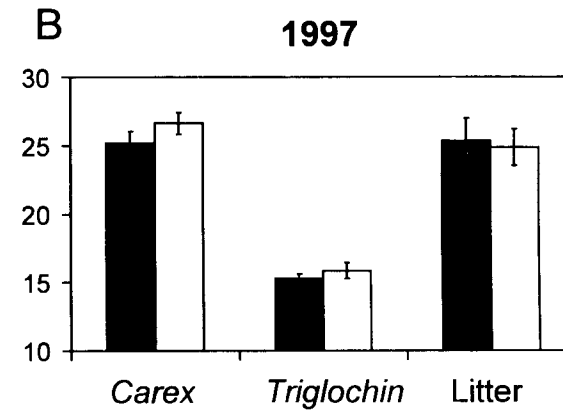
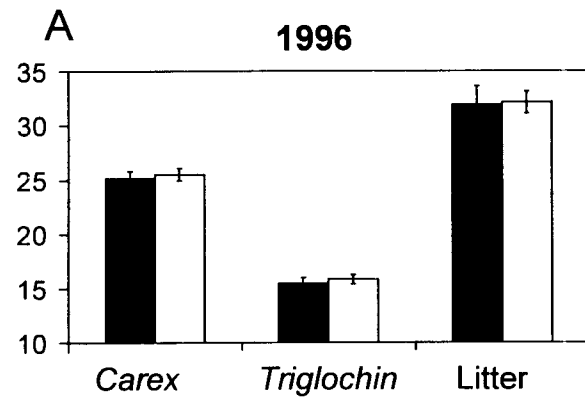
**A****Sedge Meadow Community****B****Herb Meadow Community**

FIG. 2.6. Effects of geese on plant and litter C:N ratios, sedge meadow and herb meadow communities, Susitna Flats, Alaska, August 1996 and 1997. Comparison of plots grazed by geese and those exclosed from geese in the sedge meadow community in (A) 1996 (two years of fencing) and (B) 1997 (three years of fencing), and in the herb meadow community in (C) 1996 and (D) 1997. Significant differences between grazed and exclosed plots are indicated by:

* $P \leq 0.05$, ** $P \leq 0.01$.



Sedge Meadow Community



Herb Meadow Community

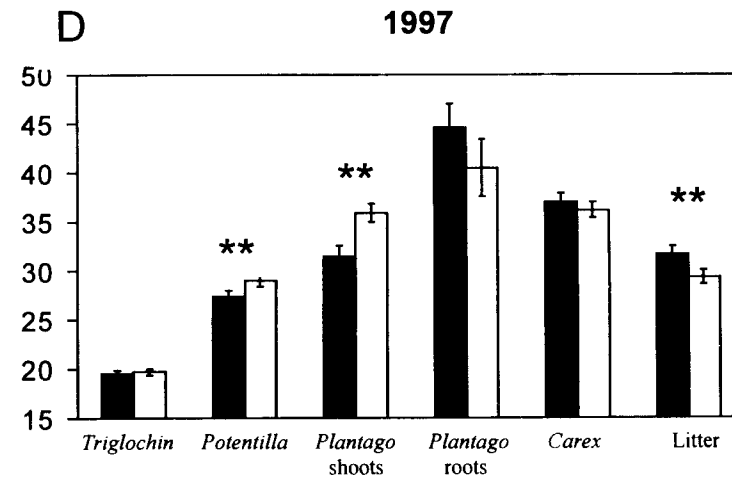
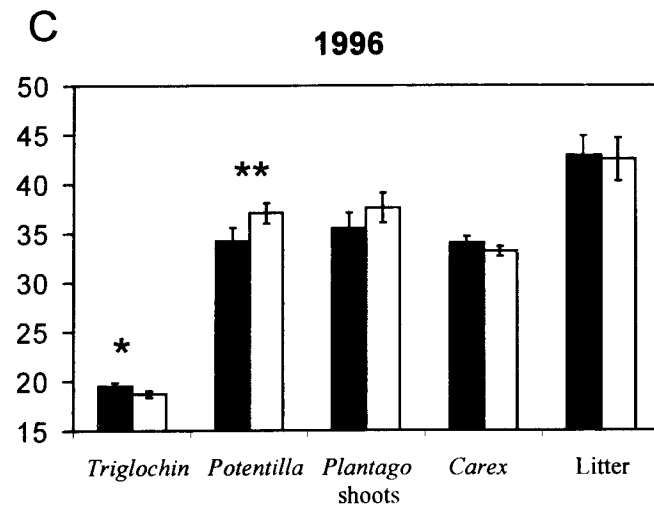
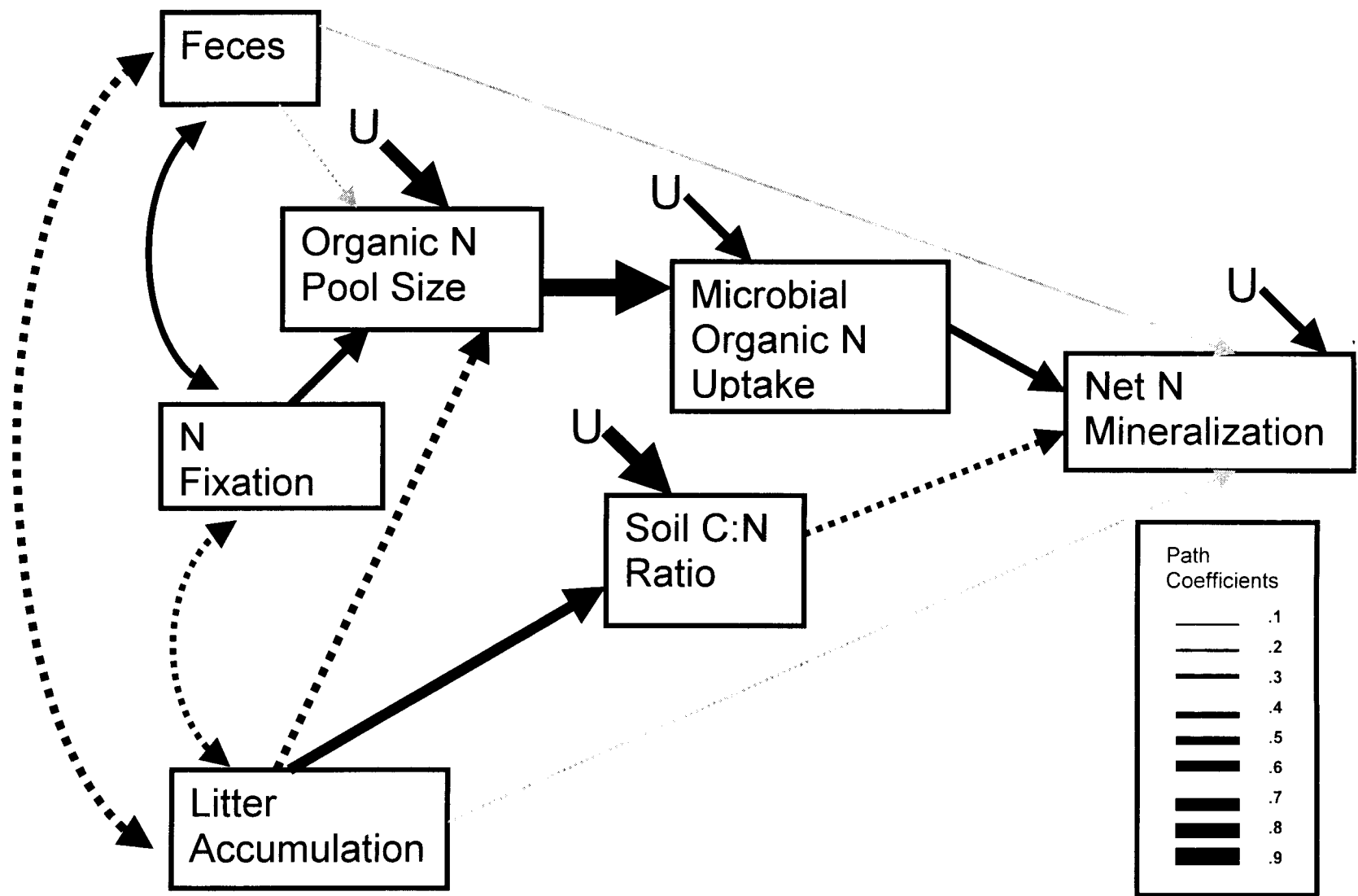


FIG. 2.7. Path diagram for net nitrogen mineralization, sedge meadow community, Susitna Flats, Alaska, May 1997. Double-headed arrows indicate correlations while single-headed arrows show causal relationships. Dashed arrows indicate negative relationships, solid arrows show positive relationships, black arrows indicate significant pathways, and grey arrows indicate non-significance. The strengths of relationships are given by path coefficients, shown by arrow width according to the legend. The unanalyzed correlation (U) was calculated as $(1-R^2)^{-1/2}$.



RESPONSE OF A SUBARCTIC SALT MARSH PLANT COMMUNITY TO GRUBBING AND GRAZING BY CAPTIVE LESSER SNOW GEESE³

Summary

1 Foraging intensity (i.e., herbivore density and duration of feeding) and faecal input are important determinants of plant community response to herbivory. We used captive adult lesser snow geese (*Anser caerulescens caerulescens*), who feed on both above- and below-ground plant tissues, to manipulate foraging intensity and faecal input to plots in a sedge meadow plant community in the spring of 1996. We measured plant and soil characteristics throughout the growing season of 1996 and in August 1997. We analysed three contrasts: grazed plots vs. ungrazed controls, plots with a short period of feeding (3 goose-hours) vs. plots with a long period of feeding (6 goose-hours), and grazed plots with faeces vs. grazed plots without faeces.

2 Although grazed plots had an order of magnitude higher foraging intensity than that imposed by wild geese in the marsh, there was no effect of grazing on biomass or nitrogen concentration in the dominant species *Carex ramenskii* and *Triglochin maritimum* after one and two growing seasons. *Carex ramenskii* had greater tiller density

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Response of a subarctic salt marsh plant community to grazing and grubbing by captive lesser snow geese.

in grazed plots compared to ungrazed controls, while *Triglochin maritimum* had greater inflorescence density and earlier senescence in grazed plots.

3 The amount of forage removed by geese did not differ between long and short period plots, indicating that geese were able to remove little additional biomass after 3 hours on plots. There were no differences in plant or soil characteristics between short and long period plots throughout the 1996 growing season and in August 1997 due to the lack of an initial treatment effect.

4 The presence of faeces had no effect on biomass or nitrogen concentration in *Carex ramenskii* or *Triglochin maritimum*. Faeces increased carbon mineralization rates throughout the 1996 growing season, but had no effect on net nitrogen mineralization. Thus faeces did not appear to increase nitrogen availability for plants in this marsh.

6 This experiment indicates that a one-time, 10-fold increase in foraging intensity in the sedge meadow community would not alter forage quality or availability for snow geese.

Keywords: Alaska, *Carex ramenskii*, forage quality and availability, foraging intensity, herbivory, *Triglochin maritimum*

Introduction

The intensity at which geese grub for below-ground plant tissues (i.e., the duration of feeding and the density of geese) is important in determining plant community response to herbivory. For example, grubbing by geese at high intensities usually reduces community biomass or the spatial extent of vegetation (e.g., Smith & Odum 1981; Giroux & Bédard 1987; Ganter *et al.* 1996; Miller *et al.* 1996; Esselink *et al.*

1997; Jano *et al.* 1998). However, low intensity grubbing may have no effect on productivity in plant communities (Giroux & Bédard 1987; Zacheis *et al.* 2000). In contrast, when geese graze on above-ground plant tissues the relationship between foraging intensity and plant community response is more complex. In arctic and subarctic goose-grazing systems, high intensity grazing has increased net above-ground primary production (NAPP; Cargill & Jefferies 1984), decreased NAPP (Gauthier *et al.* 1995), or had no effect on NAPP (Madsen & Mortensen 1987; Beaulieu *et al.* 1996; Bakker & Loonen 1998; Person *et al.* 1998). Experiments designed to vary grazing intensity by geese have similarly had mixed results, with increased NAPP at moderate grazing intensity (Hik & Jefferies 1990) or with no relationship between grazing intensity and NAPP (Zellmer *et al.* 1993).

The foraging intensity of snow geese (*Anser caerulescens*) in marshes at spring migration stopover areas is variable both spatially and temporally. Yearly snowmelt patterns at northern stopover areas can affect habitat availability, goose density, and the length of time geese will forage within an area (Hupp *et al.* 2001). Over the longer term, snow goose populations have rapidly increased in some North American flyways (Reed 1990; Ankney 1996; Abraham & Jefferies 1997), resulting in greatly increased foraging pressure along migration routes. Because foraging intensity can be highly variable at migration stopover areas, determining the relationship between intensity and plant community response to herbivory is important in evaluating the resiliency of areas to goose herbivory.

Faecal nitrogen may also affect plant community response to herbivory (Hik & Jefferies 1990). For example, in salt marshes along Hudson Bay greater NAPP in areas grazed by snow geese (Cargill & Jefferies 1984) was dependent on the addition of nitrogen in faeces (Hik & Jefferies 1990). Uric acid in goose faeces can be rapidly converted extracellularly to ammonium by soil ureases (Haynes 1986; Thomas *et al.* 1988; McNaughton *et al.* 1997; Wilson *et al.* 1999), increasing nitrogen availability to plants. In addition, animal excreta may increase nitrogen availability to plants by increasing rates of net nitrogen mineralization (Pastor *et al.* 1993; Zaady *et al.* 1996). If plant communities are nitrogen limited, greater nitrogen availability may ameliorate negative effects of herbivory, resulting in higher quality or more abundant forage for herbivores (Bazely & Jefferies 1985; Day & Detling 1990; Hik & Jefferies 1990).

We studied the effects of herbivory using captive adult lesser snow geese (*A. c. caerulescens* L.) in a salt marsh in Alaska used by wild geese during spring migration. Use of captive birds allowed us to manipulate the intensity of herbivory (i.e., goose-hours plot⁻¹) and faecal input to plots to determine if these factors played a role in plant community response to herbivory. Our experiment was conducted in the spring, when little above-ground biomass was present. Captive geese initially grazed on above-ground shoots, but when availability of these was reduced, geese grubbed for below-ground plant tissues. The objectives of the experiment were (i) to investigate the effects of herbivory on plant biomass, tiller density, and nitrogen concentration at foraging intensity higher than that imposed by wild geese; (ii) to determine if plant

response to herbivory differed between two levels of foraging intensity; and (iii) to determine if faecal nitrogen affected vegetation and soils in grazed plots.

Study Area

We conducted this study in Susitna Flats, a salt marsh in Cook Inlet, Alaska (61°15' N, 150°30' W). Cook Inlet is used as a stopover area by lesser snow geese, and Taverner's (*Branta canadensis taverneri* Delacour) and cackling Canada geese (*B. c. minima* Ridgway) during spring migration in April and May. Although 100,000 or more geese may stage in Upper Cook Inlet in the spring (Butler & Gill 1987), grazing intensity is light because geese remain in the area only 10-25 days (Zacheis *et al.* 2000), and flocks typically use individual sites only 2-3 days (Hupp *et al.* 2001). Canada geese feed mainly on the small amount of above-ground shoot biomass available early in the spring, whereas 69% of the snow goose diet consists of below-ground plant material (Zacheis *et al.* 2000). Geese do not return in the autumn, except for small numbers of Canada geese that feed along the coastal fringe of the marsh. No geese nested or reared broods in our study area. Snow geese that migrate through Cook Inlet nest on Wrangel Island, Russia. This population is less than 50% of historic levels and has not increased in recent years (Kerbes *et al.* 1999), but the potential for a population increase exists. The population of cackling Canada geese has increased 12% annually since 1988 (Wilkens & Cooch 1999).

Our experiment was conducted in a sedge meadow plant community dominated by a sedge, *Carex ramenskii* Kom. and a forb, *Triglochin maritimum* L. (nomenclature

follows Hultén 1968), with only about 2% other forbs and grasses. *C. ramenskii* and *T. maritimum* are important components of both Canada and snow goose diets (Zacheis *et al.* 2000). Feeding by wild geese in this community in the spring did not affect community composition, above- or below-ground biomass, or tiller density measured at the end of the growing season (Zacheis *et al.* 2000). Faecal nitrogen input from geese was very small, and did not affect nitrogen mineralization rates in soils or shoot nitrogen concentrations in vegetation (A.B. Zacheis, unpublished manuscript). Trampling by wild geese incorporated litter into the soil and reduced the thickness of the litter mat (Zacheis *et al.* 2000). This resulted in greater net nitrogen mineralization rates in grazed plots through effects on organic nitrogen pools, soil C:N ratios, and nitrogen fixation by cyanobacteria (A.B. Zacheis, unpublished manuscript).

Methods

EXPERIMENTAL DESIGN

We used human-imprinted adult lesser snow geese to conduct our grazing experiment. Geese were collected as goslings or eggs at the Anderson River nesting colony, Northwest Territories in 1989 (see Hupp *et al.* 1996 for details). All procedures involving geese were approved by the Animal Care and Use Committee at the University of Alaska Fairbanks.

In August 1995, we set up five groups (blocks) of five 2 m x 2 m plots in the sedge meadow community. Plots within a block were in similar vegetation based on visual cover estimates. Blocks were within 1 km of each other. We erected fences

around the plots in the spring of 1996 and 1997 to exclude wild geese.

We conducted the experiment from 25 April through 6 May 1996, coincident with the time wild geese were at Susitna Flats, and within 7 days after snow had melted from plots. Plots within a block were randomly assigned one of five treatments: control (no feeding), short period of feeding with faecal input, short period without faeces, long period of feeding with faeces, and long period without faeces. In the feeding treatments, two or three geese were put on a plot, and the amount of time a single randomly selected goose spent feeding was recorded. We observed a different bird every 10 minutes. Feeding behaviour included grazing on above-ground shoots, and digging for and ingesting below-ground plant tissues. We removed geese from plots when the total time spent feeding was 2 or 3 hours for the long period treatment (depending on whether two or three geese were used) for a total of 6 goose-hours. Short period treatments had a total of 3 goose-hours. For the treatments without faeces, geese were fasted for 2-8 hours before being placed on plots. Fasted geese usually fed for 1 hour before defecating, after which geese were removed, and other fasted birds were placed on the plots or the trial was continued later after geese had been fed and fasted again. For treatments with faeces, geese were allowed to feed on native vegetation for a minimum of 1 hour before being placed on plots, so that geese were defecating at normal rates. We did not impose additional grazing bouts at later dates because sites in Cook Inlet were typically subjected to a single period of exploitation by snow geese over a 2-3 day interval in the spring (Hupp *et al.* 2001).

VEGETATION SAMPLING

To estimate the amount of forage removed by geese from a plot ("offtake"), we sampled vegetation in plots immediately before and after a trial. We divided plots into 48 12.5 cm x 25 cm subplots, excluding a 50 cm walkway in the centre and a 25 cm border around the edges. Three subplots were sampled immediately before (pre-treatment) and after (post-treatment) trials, with subplots adjacent to those already sampled left undisturbed. Subplots were excavated to a depth of approximately 10 cm, washed in the field to remove most of the soil, and re-washed in fresh water in the field laboratory. We sampled green shoots of *T. maritimum* where they emerged from the taproot, and *C. ramenskii* shoots at the point they joined below-ground rhizomes. In both species, more than 50% of the shoot biomass was below the soil surface. Geese eat entire shoots of these plant species, including basal portions (Zacheis *et al.* 2000). Samples were frozen, shipped to the University of Alaska, dried to constant mass at 60 °C, and weighed (± 0.001 g). Offtake was the difference between pre- and post-treatment samples.

In August 1995 we clipped above-ground biomass to a height of 1 cm in three of the 12.5 cm x 25 cm subplots in each plot for an estimate of pre-treatment differences. Above-ground biomass was clipped from four subplots in each plot in July 1996, and in August 1996 and 1997. Litter was collected from the soil surface in the clipped subplots in August of each year. Samples were washed in fresh water, dead material was sorted from live, and live material was sorted by species. Samples were frozen for shipping, later dried to constant mass at 60 °C, and weighed (± 0.01 g). *T. maritimum* and *C. ramenskii* from July and August 1996 were ground in a 20-mesh size Wiley Mill and

combusted for total nitrogen in a LECO CNS 2000 Elemental Analyzer (St. Joseph, Missouri, USA).

We estimated tiller and inflorescence density in August 1996 and 1997 by counting the number of tillers and inflorescences of the dominant species in a 9 cm x 12.5 cm section of each of the four subplots sampled in each plot. A “tiller” was defined as a culm for *C. ramenskii* and a group of leaves emerging from the soil for *T. maritimum*.

FAECAL SAMPLING

We estimated the total number of faeces deposited on a plot by tallying faeces produced during a trial by a single goose, multiplied by the number of geese per plot. We tallied faecal production on the same randomly selected geese on which we monitored feeding behaviour, selecting a different goose every 10 minutes. To estimate carbon and nitrogen input to soil from faeces, we collected fresh faeces from captive geese after they had fed for at least 24 hours on salt marsh vegetation. Geese were in a pen with a floor so faeces were not trampled into the soil. All faeces were collected within 5 minutes of deposition. We estimated mean dry weight of faeces from a sample of 25 intact, air-dried droppings collected over several days. Faeces were air-dried and combusted in a LECO CNS 2000 Elemental Analyzer to determine percent total carbon and nitrogen. Total carbon and nitrogen input per plot is the product of number of faeces per plot, the percent carbon or nitrogen in faeces, and the mean dry weight of faeces. To estimate extractable nitrogen deposited on plots, other fresh faeces were immediately placed in 2N KCl. To inhibit microbial growth, phenylmercuric acid was added to the extract after filtering and

before freezing. Extracts were analysed for $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ (extractable inorganic nitrogen) on a Lachat Quikchem AE Automated Ion Analyzer (Milwaukee, Wisconsin, USA). Extractable nitrogen per plot is the product of number of faeces per plot, extracted nitrogen per gram dry weight faeces, and mean dry weight per faecal pellet.

SOIL SAMPLING

To examine the effects of geese on carbon and nitrogen mineralization in soils, we collected soil cores from plots before experimental trials (for an estimate of pre-treatment differences between plots), immediately after trials (May samples), and in July and August 1996. Cores were 5 cm deep and 5.5 cm in diameter, with three collected from randomly selected subplots in each plot at each sampling date. Cores were kept cool and shipped to the University of Alaska, where they were divided into three vertical sections. One section of each core was dried for soil water content, ground in a coffee grinder, and combusted in a LECO CNS 2000 Elemental Analyzer for total carbon and nitrogen. Another section was extracted with 2N KCl for determination of initial extractable inorganic nitrogen levels ($\text{NH}_4^+\text{-N}$ plus $\text{NO}_3^-\text{-N}$). We incubated the third section in a 1 litre jar at 15 °C for three weeks, at which time samples were again extracted for inorganic nitrogen. Phenylmercuric acid was added to extracts to inhibit microbial growth, and extracts were frozen until analysis for $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ on a Lachat Quikchem AE Automated Ion Analyzer. Net nitrogen mineralization per gram dry weight soil is the difference in inorganic nitrogen between final and initial samples, divided by the number of days of incubation.

Carbon mineralization was measured by sampling incubation jars for CO₂-C at weekly intervals during the incubations. Jars were fitted with rubber septa through which gas samples were removed using a syringe. Samples were analysed on a GC-8A gas chromatograph (Shimadzu, Tokyo, Japan) for CO₂-C. Jars were vented after each weekly sample. Carbon mineralization is the sum of the CO₂-C per gram dry weight soil evolved over the three weekly periods, divided by the number of days of incubation.

STATISTICAL ANALYSIS

We used a repeated measures MANOVA model to analyse data collected several times throughout 1996 (soil characteristics in May, July, and August 1996; biomass and nitrogen concentration of *C. ramenskii* and *T. maritimum* in July and August 1996) and 1997 (standing dead biomass, litter, and tiller and inflorescence density in August 1996 and 1997). The model had subplots nested within blocks. To test for treatment effects, we analysed three pre-planned contrasts: all plots in which geese fed (i.e., long and short period plots combined; termed “grazed” plots) vs. ungrazed control plots, long period of feeding plots vs. short period plots, and grazed plots with faeces vs. grazed plots without faeces. We term these contrasts the grazing, duration of grazing, and faeces contrasts, respectively. Because contrasts are orthogonal (Kuehl 1994), per-comparison error rates are appropriate, and no correction was made to control experiment-wise error rate (Day & Quinn 1989). We also tested for a time effect (month or year), and a time x contrast interaction. If a contrast or a time x contrast interaction was significant, we analysed

individual monthly ANOVAs, using a Bonferroni correction ($0.05/\text{number of sampling periods}$) to establish a critical α -value (von Ende 1993).

Because biomass of *C. ramenskii* and *T. maritimum* was measured at unequal intervals throughout 1996 and 1997 (July 1996, August 1996, August 1997), all measurements could not be included in a single repeated measures analysis. We analysed the July and August 1996 data with a repeated measures, and analysed August 1997 data in a separate univariate ANOVA, using a Bonferroni correction ($0.05/3 \text{ sampling periods} = 0.017$) to set a critical α -value.

We checked for initial differences between plots by testing for an overall treatment effect in biomass (using August 1995 samples), in total soil carbon and nitrogen, and in carbon and nitrogen mineralization (using 1996 pre-treatment samples taken in April and May 1996) with an ANOVA model nesting subplots within blocks.

We used a one-tailed signed rank test to determine if offtake in long period plots, in short period plots, and in all grazed plots (long and short period plots combined) was significantly greater than zero. We analysed the effect of length of grazing period on offtake using the blocked ANOVA model described above.

In all analyses, data were transformed ($\log_e + 1$, inverse + 1, or square root + $3/8$) to correct for heterogeneity of error variance if necessary (Neter *et al.* 1990; Zar 1996). We also ran analyses on ranked data, creating distribution-free tests, as transformations did not guarantee that parametric model assumptions were met (Conover 1980). We report results on transformed data, noting those cases where analyses on ranked data produced substantially different results. All statistical calculations were done in SAS v. 8

(SAS Institute Inc., Cary, North Carolina, USA). Non-transformed means \pm 1 SE are reported throughout.

Results

PRE-EXPERIMENT DIFFERENCES

There were no differences between plots in above-ground biomass or litter in August 1995, before the experiment was initiated (*C. ramenskii*: $F_{4,56} = 0.38$, $P = 0.82$; *T. maritimum*: $F_{4,56} = 0.03$, $P = 0.99$; litter: $F_{4,56} = 0.31$, $P = 0.87$). Similarly, there were no differences between soils collected on plots in 1996 before treatments for total soil carbon ($F_{4,54} = 0.80$, $P = 0.53$), soil nitrogen ($F_{4,54} = 0.75$, $P = 0.56$), carbon mineralization ($F_{4,56} = 0.32$, $P = 0.86$), or nitrogen mineralization ($F_{4,56} = 0.75$, $P = 0.56$).

FORAGING INTENSITY AND FAECAL INPUT

Total offtake in long period and short period plots combined ("grazed" plots) averaged 5.52 g dwt m⁻² (Fig. 1A), 18% of the available biomass. Total offtake was not different between long and short period plots (Fig. 1A; $F_{1,44} = 0.01$, $P = 0.90$). *C. ramenskii* offtake in all grazed plots averaged 3.59 g dwt m⁻² (Fig. 1B), 20% of the available biomass. Again, offtake did not differ between long and short period treatments (Fig. 1B; $F_{1,44} = 0.73$, $P = 0.40$), and only the long period plots had forage removal significantly greater than zero (Fig. 1B). *T. maritimum* offtake in all grazed plots was

16% of the available biomass, or $1.93 \text{ g dwt m}^{-2}$ (Fig. 1C). Offtake in long and short period plots did not differ from zero, or from each other (Fig. 1C; $F_{1,44} = 0.88$, $P = 0.35$).

Plots (4 m^2) with faeces received an average of 71.3 ± 10.7 faeces. Faeces were $20.83 \pm 1.29 \%$ carbon and $1.080 \pm 0.114 \%$ nitrogen, with 10% of the nitrogen as NH_4^+ . Faecal additions to plots, on a m^2 basis, were $0.071 \pm 0.011 \text{ g}$ total N, $0.007 \pm 0.001 \text{ g}$ NH_4^+ -N, and $1.36 \pm 0.21 \text{ g}$ C.

The number of faeces on plots was highly correlated with the length of time geese were on plots ($r = 0.40$, $P = 0.0001$). The number of faeces was correlated with *C. ramenskii* offtake ($r = 0.22$, $P = 0.05$) and with total offtake ($r = 0.22$, $P = 0.06$), but correlations between time on plots and offtake were not significant (*C. ramenskii*: $r = 0.19$, $P = 0.11$; total offtake: $r = 0.18$, $P = 0.13$). *T. maritimum* offtake was not correlated with either number of faeces ($r = 0.02$, $P = 0.87$) or time on plots ($r = 0.01$, $P = 0.94$).

GRAZING CONTRAST (GRAZED VS. UNGRAZED PLOTS)

There were no overall differences in *T. maritimum* or *C. ramenskii* biomass between all grazed plots (long and short period plots combined) and ungrazed controls in 1996 (Table 1, Fig. 2A, D). However, there was a significant interaction between this contrast and time for *T. maritimum* (Table 1). Grazed plots had slightly, but not significantly, greater *T. maritimum* biomass in July, whereas ungrazed controls had greater biomass in August (significant on the ranks only: $F_{1,76} = 7.51$, $P = 0.008$; Fig. 2D). Grazed plots lost green biomass between July and August, whereas ungrazed plots continued to add biomass (Fig. 2D). In August 1997, two growing seasons following

treatments, there were no differences between grazed and ungrazed plots for either plant species (*C. ramenskii*: $F_{1, 76} = 0.18$, $P = 0.67$; *T. maritimum*: $F_{1, 76} = 0.46$, $P = 0.50$).

C. ramenskii had more tillers in grazed plots, with the greatest difference between treatments apparent after two growing seasons (Table 1, Fig. 3A). The significant year x contrast interaction for *T. maritimum* tillers was due to slightly more tillers in grazed plots in 1997 (Table 1, Fig. 3D); however, this difference was not significant. *T. maritimum* had more inflorescences in grazed plots, with the largest difference in 1997 (Table 1, Fig. 4D). There was no significant effect of grazing on inflorescence density of *C. ramenskii* (Table 1, Fig. 4A).

Grazing did not affect shoot nitrogen concentration in either *C. ramenskii* or *T. maritimum* (Table 1, Fig. 5A, D). A significant month x contrast interaction for both species (Table 1) was due to vegetation in ungrazed plots showing a greater decline in nitrogen concentration between July and August than vegetation in grazed plots (Fig. 5A, D).

There was no overall difference in standing dead biomass between grazed and ungrazed plots (Table 1). However, there was more standing dead biomass in grazed plots in August 1997, but not in 1996 (Fig. 6A), resulting in a significant year x contrast interaction (Table 1). A multiple regression ($r^2 = 0.48$, $P = 0.0001$) found standing dead biomass in 1997 to be strongly related to *T. maritimum* biomass ($t = 8.78$, $P = 0.0001$), and positively related to *C. ramenskii* biomass ($t = 1.83$, $P = 0.07$), tiller density of *C. ramenskii* ($t = 3.02$, $P = 0.003$) and tiller density of *T. maritimum* ($t = 2.46$, $P = 0.02$). In contrast to standing dead biomass, litter biomass was greater in ungrazed plots, with the

largest effect in 1996 (Table 1, Fig. 6D). There was no effect of the grazing treatment on total soil carbon and nitrogen (Table 2), carbon mineralization (Table 2, Fig. 7A), or nitrogen mineralization (Table 2, Fig. 7D).

DURATION OF GRAZING CONTRAST (LONG VS. SHORT PERIOD PLOTS)

There were no significant differences between long and short period plots in *C. ramenskii* and *T. maritimum* biomass in 1996 (Table 1, Fig. 2B, E) or in 1997 (*C. ramenskii*: $F_{1,76} = 1.15$, $P = 0.29$; *T. maritimum*: $F_{1,76} = 0.34$, $P = 0.56$). In addition, tiller density (Fig. 3B, E), inflorescence density (Fig. 4B, E) and shoot nitrogen concentration (Fig. 5B, E) did not show a treatment effect (Table 1). There was a significant time x contrast interaction for tiller density in *C. ramenskii*, due to opposite trends in 1996 and 1997 (Table 1, Fig. 3B); however, contrast differences were not significant in either year. There was no effect of the duration of grazing on either standing dead (Table 1, Fig. 6B) or litter biomass (Table 1, Fig. 6E). Finally, there were no differences between long and short period plots for total soil carbon or nitrogen (Table 2), carbon mineralization (Table 2, Fig. 7B), or nitrogen mineralization (Table 2, Fig. 7E).

To determine whether differences between grazed and ungrazed plots found in this experiment (i.e., differences in *C. ramenskii* tiller density, *T. maritimum* inflorescence density, and litter biomass) were apparent when plots were grazed for only 3 hours, we compared short period plots and controls in separate repeated measures analyses. *C. ramenskii* tiller density ($F_{1,76} = 6.17$, $P = 0.02$) and *T. maritimum*

inflorescence density ($F_{1, 76} = 7.49, P = 0.01$) were significantly greater, and litter biomass was significantly less ($F_{1, 75} = 32.87, P = 0.0001$) in short period plots compared to ungrazed controls.

FAECES CONTRAST (FAECES VS. NO FAECES PLOTS)

The addition of faeces had no effect on the biomass of *C. ramenskii* or *T. maritimum* in 1996 (Table 1, Fig. 2C, F) or 1997 (*C. ramenskii*: $F_{1, 76} = 1.13, P = 0.29$; *T. maritimum*: $F_{1, 76} = 3.37, P = 0.07$). There were more *C. ramenskii* tillers in plots with faeces (Table 1, Fig. 3C), but there was no effect of faeces on tillering in *T. maritimum* (Table 1, Fig. 3F). The faeces treatment did not affect inflorescence density (Table 1, Fig. 4C, F) or nitrogen concentration (Table 1, Fig. 5C, F) for either species. There was a month x contrast interaction in *T. maritimum* nitrogen concentration due to opposite trends in plots with and without faeces (Table 1, Fig. 5F). Faecal addition did not affect standing dead biomass (Table 1, Fig. 6C), but plots with faeces had less litter than those without (Table 1, Fig. 6F).

Carbon mineralization was greater in plots with faeces than without faeces (significant on the ranks only: $F_{1, 56} = 5.00, P = 0.03$; Table 2, Fig. 7C). The faeces treatment did not affect nitrogen mineralization (Table 2, Fig. 7F) or total soil carbon and nitrogen (Table 2).

Discussion

FORAGING INTENSITY

Captive snow geese grazed above-ground shoots of both *C. ramenskii* and *T. maritimum*, which were quickly depleted as less than 15 g dwt m⁻² of above-ground biomass was available on plots. (Although we estimated 30 g dwt m⁻² of shoot biomass in pre-treatment plots, we included portions of shoots below the soil surface in these measurements, which probably accounted for more than 50% of shoot biomass). Geese fed almost continuously on plots initially, but feeding slowed after approximately 1 hour when the majority of shoots appeared to have been consumed. At that point, geese spent more time grubbing for below-ground portions of *T. maritimum* and may have occasionally fed on below-ground shoot tissue and rhizomes of *C. ramenskii*. *T. maritimum* plants were difficult for geese to remove, due to a large, firmly rooted taproot. Geese discarded *T. maritimum* taproots covered with dead material, and fed instead on below-ground portions of shoots that emerged from root crowns and on the root crown itself. Grubbing therefore involved a large time and energy expenditure for geese, and yielded only a small proportion of uprooted biomass that was ingested. Because of the difficulty in extracting below-ground material, wild geese fed primarily on above-ground shoots in the sedge meadow community (Zacheis *et al.* 2000). In contrast, wild geese fed extensively on roots of *Plantago maritima* L., a forb growing in the herb meadow community in Susitna Flats (Zacheis *et al.* 2000). *P. maritima* is less firmly rooted and more easily extracted from the soil than *T. maritimum*, so that grubbing for roots of *P. maritima* is an efficient feeding strategy for snow geese.

Foraging intensity in our experiment was probably considerably higher than that imposed by wild geese at Susitna Flats. By the end of the experimental trials, geese spent much time searching for food, or stopped feeding. In fact, it was difficult to accumulate 6 goose-hours of feeding on plots, as feeding slowed substantially after 3 or 4 goose-hours. Wild birds would have likely moved to other areas following the reduction of forage to the extent induced in our experiment. Based on faecal counts, grazed plots experienced an order of magnitude greater foraging intensity ($17.8 \text{ faeces m}^{-2}$) than that imposed by wild geese in the marsh in 1997 ($1.8 \text{ faeces m}^{-2}$; Zacheis *et al.* 2000). Finally, we were unable to measure any significant offtake of either *C. ramenskii* or *T. maritimum* in areas grazed by wild geese (Zacheis *et al.* 2000), but found 20% and 16% offtake, respectively, for these species in plots fed on by captive geese. Measuring offtake in large areas grazed by wild geese is naturally more difficult owing to spatial variability in vegetation and feeding patterns (Giroux & Bédard 1987; Zacheis *et al.* 2000); nevertheless, we believe the higher offtake in captive goose plots indicates a substantially greater grazing intensity.

GRAZING CONTRAST

Wild geese feeding in the spring, and captive geese foraging at 10 times the intensity of wild geese, did not affect biomass of vegetation in the sedge meadow community measured at the end of the growing season (Zacheis *et al.* 2000). Immediately after captive geese were removed from plots, significantly less biomass remained on grazed plots than on ungrazed plots; however, later in the growing season

differences between grazed and ungrazed plots disappeared, as plants were able to fully compensate for tissue loss. Graminoids such as *C. ramenskii* are generally tolerant of herbivory, with productivity often unaffected by grazing or clipping (Madsen & Mortensen 1987; Zellmer *et al.* 1993; Beaulieu *et al.* 1996; Ruess *et al.* 1997; Bakker & Loonen 1998; Person *et al.* 1998), or with greater productivity following grazing or clipping under certain conditions (Cargill & Jefferies 1984; Hik & Jefferies 1990; Hik *et al.* 1991; Ruess *et al.* 1997). Graminoids have characteristics making them well adapted to grazing, such as basal leaf meristems, protection of meristems by leaves, and carbohydrate production in undamaged tillers (Hyder 1972; Archer & Tieszen 1986; Rosenthal & Kotanen 1994). Although *T. maritimum* is a forb, it has a graminoid-like growth form, with leaf meristems located at or below the soil surface, and meristems protected by dead and live tissue. These characteristics may enable it to quickly re-grow following grazing, similar to *P. maritima*, another forb with a graminoid-like growth form, which has higher productivity when clipped at a frequency mimicking goose grazing (Prins *et al.* 1980).

T. maritimum is probably able to tolerate grubbing by snow geese due to its thick, firmly rooted taproot, which makes it difficult for snow geese to uproot entire plants. This is in contrast to other salt marsh plants where grubbing reduces the biomass or spatial extent of vegetation (e.g., Smith & Odum 1981; Bélanger & Bédard 1994; Ganter *et al.* 1996; Miller *et al.* 1996; Esselink *et al.* 1997; Hupp *et al.* 2000).

Although foraging by captive geese did not alter plant biomass later in the growing season, *C. ramenskii* and *T. maritimum* had greater tiller and inflorescence

density, respectively, in grazed plots. Zacheis *et al.* (2000) observed that grazing by wild geese in the sedge meadow community did not affect tiller density of these species, but that the inflorescence density of *C. ramenskii* increased whereas that of *T. maritimum* did not. Increased leaf or tiller production following herbivory or clipping is a common response in graminoids (Caldwell *et al.* 1981; Aarssen & Turkington 1987; Kotanen & Jefferies 1987; Olsen & Richards 1988; Bazely & Jefferies 1989; Kotanen & Jefferies 1989), and in forbs such as *Triglochin palustris* (Mulder & Ruess 1998), due to either activation of quiescent axillary buds, or to re-growth from already activated meristematic tissue (Hyder 1972). Re-growth from axillary buds is often slow (Hyder 1972; Olson & Richards 1988) and may explain why increases in tiller and inflorescence density became most pronounced two growing seasons following treatments. Although *C. ramenskii* had more tillers, biomass was not different between plots, suggesting that plants may have become shorter. Reduction of stature to a more prostrate growth form under herbivory is a common response in grazing-tolerant plants (Gray & Scott 1980; Coughenour 1985; Painter *et al.* 1993), including *C. ramenskii* (B.T. Person, unpublished manuscript).

Leaves of *T. maritimum* senesced earlier in plots grazed by geese compared to ungrazed controls. Grazed plants lost green biomass between July and August 1996 due to tissue senescence, while ungrazed plants continued to add green biomass. In August 1997, there was significantly more standing dead biomass in grazed compared to ungrazed plots. Standing dead was strongly related to *T. maritimum* biomass in a multiple regression (see Results), so we infer that, again, tissue was senescing earlier in grazed plots compared to ungrazed controls. Grazing can decrease leaf lifespan in

graminoids (Kotanen & Jefferies 1987; Bazely & Jefferies 1989; Kotanen & Jefferies 1989), but alternatively may delay leaf senescence in some forbs and grasses (Nowak & Caldwell 1984; Peterson *et al.* 1992; Meyer 1998).

The amount of litter on soil surfaces was reduced in grazed areas. Although we did not measure litterfall directly, standing crop biomass and relative species abundance did not differ among plots at the end of the growing season in 1995, so we infer that litter production was the same between grazed and ungrazed plots. The loss of litter in grazed plots was due to geese trampling it into wet, muddy soils in the spring, a strong effect also seen in the portions of the marsh grazed by wild birds (Zacheis *et al.* 2000). Incorporating litter into soils through trampling by wild geese increased organic nitrogen pool size, decreased soil C:N ratio, and facilitated the growth of nitrogen-fixing cyanobacteria on bare, trampled soils (A.B. Zacheis, unpublished manuscript). These factors led to greater rates of net nitrogen mineralization in grazed areas compared to ungrazed (A.B. Zacheis, unpublished manuscript). In contrast, in this experiment we did not find greater nitrogen mineralization or lower soil C:N ratios on grazed plots. We measured effects of wild geese on soil characteristics in paired grazed and exclosed plots after grazing had been excluded from the latter for 3 years. However, similar measurements in this study were made after only 1 year of treatment. Grazing effects on soil nutrient cycles may extend for more than 1 year after herbivores are excluded, thus requiring several years for differences between grazed and exclosed plots to become apparent. This may be particularly true of characteristics such as soil C:N ratios, where

small additions of nitrogen to soils through the effects of grazing are masked by a relatively large pool of total soil nitrogen.

DURATION OF GRAZING CONTRAST

Offtake biomass of *C. ramenskii* and *T. maritimum* (biomass removed by geese) did not differ between long and short period plots. Feeding after 3 hours may have resulted in little additional forage removal, because geese were grubbing and may have spent more time probing than ingesting plant material (both activities were recorded as feeding behaviours). Our experimental procedure increased one measure of foraging intensity, goose-hours m^{-2} , but did not increase another measure of foraging intensity, the amount of biomass removed by geese. Correlations between goose-hours and offtake were not significant (see Results), indicating that these two measures of foraging intensity were not closely related. As offtake measurements demonstrate an actual effect of goose foraging, they are probably more appropriate estimates of foraging intensity than time feeding (goose-hours) in experiments where levels of foraging intensity are compared.

The lack of differences between long and short period plots for any plant characteristic measured throughout the growing seasons of 1996 and 1997 suggests that effects of herbivory in the sedge meadow would result as readily from a short period of feeding as from a longer period. In fact, significant differences between grazed and ungrazed plots in this experiment (more *C. ramenskii* tillers and *T. maritimum* inflorescences, and less litter in grazed plots) were also significantly different between

short period plots and ungrazed controls (see Results), indicating that 3 goose-hours plot⁻¹ was sufficient to produce a grazing effect. Sedge meadow habitats at Susitna Flats are likely grazed by wild geese for only short periods due to the relatively small amount of forage biomass present. Snow geese use areas in Cook Inlet for brief periods (Hupp *et al.* 2001) compared to geese at stopover areas where forage biomass is greater (Giroux & Bédard 1987; Esselink *et al.* 1997) or where growing plants replace tissue lost to grazing (Prins *et al.* 1980).

FAECES CONTRAST

Faecal nitrogen did not increase plant nitrogen concentrations or vegetation biomass in the portions of the sedge meadow community grazed by wild geese, probably because faecal inputs were very small (A.B. Zacheis, unpublished manuscript). In this experiment, increasing faecal nitrogen input to plant communities by an order of magnitude still did not result in higher shoot nitrogen concentrations or greater plant biomass. Faeces may not provide an important nitrogen source to plants in the early spring, as early season growth in deciduous perennials may rely more on nitrogen stores in below-ground tissues than in uptake from soil solution (Chapin 1980). Alternatively, faecal nitrogen may not be an important source of nitrogen because the amount added to plots was small compared to other nitrogen sources in soils. The soluble nitrogen (NH_4^+) contained in faeces was only 1% (0.007 g N m^{-2}) of the NH_4^+ mineralised in the top 5 cm of soil during the first 30 days following treatments ($0.666 \text{ g NH}_4^+ \text{-N m}^{-2}$). The total nitrogen in faeces (0.071 g N m^{-2}) was only 0.1% of the total soil nitrogen in the top 5 cm

of soil (61 g N m^{-2}). In studies where goose faeces or ungulate urine alone (Bazely & Jefferies 1985; Thomas *et al.* 1988; Day & Detling 1990; Thomas *et al.* 1990), or in combination with grazing (Hik & Jefferies 1990) have increased biomass and nitrogen concentrations in vegetation, excretory nitrogen additions were typically much greater than in our experiment (up to 52 g N m^{-2} ; Thomas *et al.* 1986; Thomas *et al.* 1988; Day & Detling 1990; Hik & Jefferies 1990). In Susitna Flats, the addition of nitrogen as slow release fertiliser (10 g N m^{-2} or 140 times that in the captive goose study) did result in increased *C. ramenskii* and *T. maritimum* biomass (A.B. Zacheis, unpublished data). As other plants species and microbes may compete for faecal nitrogen (Gauthier *et al.* 1995; Beaulieu *et al.* 1996; Kaye & Hart 1997), a large amount of nitrogen may be required to elicit a vegetation response. However, our experiment was at a high grazing intensity for Susitna Flats, and greater faecal nitrogen additions than those produced in this study are probably not realistic in a natural setting.

Neither faeces produced by wild geese (A.B. Zacheis, unpublished manuscript) nor the 10-fold greater faecal nitrogen input in this study affected nitrogen mineralization rates. Again, this is probably because these inputs are very small (only 0.1% of the total soil nitrogen in this experiment). In studies where faeces affected mineralization rates (either an increase or a decrease), faecal nitrogen additions were 4-45% of the total soil nitrogen (Ruess & McNaughton 1987; Pastor *et al.* 1993). In grazing ecosystems, greater net nitrogen mineralization rates in grazed areas have been attributed to faecal nitrogen input when dung deposits are large (up to $4.6 \text{ g N m}^{-2} \text{ year}^{-1}$; Frank & McNaughton 1992; Frank & Groffman 1998). If faecal nitrogen additions to soil are large enough to

substantially decrease the C:N ratio of the substrate on which microbes feed, net mineralization will be greater in areas with faecal deposition.

In contrast, the small amount of carbon added as faeces (1.36 g C m^{-2}) increased carbon mineralization rates, although additions were only 0.2% of the total soil carbon in the top 5 cm of soil (894 g C m^{-2}). The addition of this easily decomposable, low C:N (20:1) substrate to soil increased microbial activity as measured by CO_2 evolution rate, an effect commonly found in dung-amended soils (Ruess & McNaughton 1987; Pastor *et al.* 1993). In Susitna Flats, faecal additions in the spring raised carbon mineralization rates throughout the growing season, indicating that faeces may decompose slowly (Bazely & Jefferies 1985) or that faeces may prime long-lasting microbial activity.

IMPLICATIONS FOR GEESE

In Susitna Flats, geese follow and feed along the edge of the melting snow pack in the spring (Hupp *et al.* 2001), so that foraging intensity is spatially variable both within and among years due to snowmelt patterns. Exposed vegetation near snow may be intensively fed upon, whereas vegetation under the snow or in snow-free areas is not exploited. Because of this variability in use patterns, some areas of the sedge meadow community may be more heavily exploited than others, or the community as a whole may experience higher foraging intensities in years of favourable snowmelt patterns. Our captive goose experiment and results of Zacheis *et al.* (2000) indicate that the sedge meadow community is resilient to widely varying levels of exploitation, and that increasing intensity by an order of magnitude for 1 year would not affect plant biomass or

forage availability for geese. In addition, the experiment demonstrates that feeding by geese in the sedge meadow did not increase forage quantity or quality for the herbivore, as has been observed in other goose-grazing systems (e.g., Ydenberg & Prins 1981; Cargill & Jefferies 1984; Hik & Jefferies 1990; Hik *et al.* 1991; Gauthier *et al.* 1995; Beaulieu *et al.* 1996). In contrast, in an herb meadow community within Susitna Flats, foraging by wild geese reduced the availability of the forage species *P. maritima* but increased biomass of *C. ramenskii* (Zacheis *et al.* 2000). Increased foraging pressure in the herb meadow community could substantially impact forage availability, so that this plant community does not show the stability of the sedge meadow to herbivory by geese.

Our experiment also suggests that the sedge meadow community would not be affected should an increase in the snow goose population result in higher foraging intensity than currently exists. However, we only increased foraging intensity for one spring, and larger populations would create a long-term increase in foraging pressure. A long-term study, with repeated bouts of high intensity foraging, is necessary to determine the effects of sustained use by large populations of geese.

Conclusion

We conclude that the sedge meadow community is not affected by varying levels of foraging by snow geese because (1) plants are exploited at a very early stage of growth, (2) low plant biomass limits the duration for which geese are able to exploit sites, (3) the dominant plant species are highly resilient to herbivory and (4) nutrient inputs from faecal deposition are small.

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References

- Aarssen, L.W. & Turkington, R. (1987) Responses to defoliation in *Holcus lanatus*, *Lolium perenne*, and *Trifolium repens* from three different-aged pastures. *Canadian Journal of Botany*, **65**, 1364-1370.
- Abraham, K.F. & Jefferies, R.L. (1997) High goose populations: causes, impacts and implications. *Arctic Goose Habitat Working Group Report* (ed. B. Batt), pp. 7-72. Arctic Goose Joint Venture Special Publication, U.S. Fish and Wildlife Service, Washington, D.C., and Canadian Wildlife Service, Ottawa, Ontario.
- Ankney, C.D. (1996) An embarrassment of riches: too many geese. *Journal of Wildlife Management*, **60**, 217-223.
- Archer, S.R. & Tieszen, L.L. (1986) Plant responses to defoliation: hierarchical considerations. *Grazing Research at Northern Latitudes* (ed. O. Gudmundson), pp. 45-59. Plenum Press, New York, New York.
- Bakker, C. & Loonen, M.J.J.E. (1998) The influence of goose grazing on the growth of *Poa arctica*: overestimation of overcompensation. *Oikos*, **82**, 459-466.
- Bazely, D.R. & Jefferies, R.L. (1985) Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. *Journal of Applied Ecology*, **22**, 693-703.
- Bazely, D.R. & Jefferies, R.L. (1989) Leaf and shoot demography of an arctic stoloniferous grass, *Puccinellia phryganodes*, in response to grazing. *Journal of Ecology*, **77**, 811-822.

- Beaulieu, J., Gauthier, G. & Rochefort, L. (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology*, **84**, 905-914.
- Bélanger, L. & Bédard, J. (1994) Role of ice scouring and goose grubbing in marsh plant dynamics. *Journal of Ecology*, **82**, 437-445.
- Butler, W.I. Jr. & Gill, R.E. (1987) *Spring 1986 Aerial Surveys of Geese and Swans Staging in Upper Cook Inlet*. U.S. Fish and Wildlife Service, Anchorage, Alaska.
- Caldwell, M.M., Richards, J.H., Johnson, D.A., Nowak, R.S. & Dzurec, R.S. (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia*, **50**, 14-24.
- Cargill, S.M. & Jefferies, R.L. (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 669-686.
- Chapin, F.S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233-260.
- Conover, W.J. (1980) *Practical Nonparametric Statistics*, 2nd edn. John Wiley & Sons, New York, New York.
- Coughenour, M.B. (1985) Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden*, **72**, 852-863.
- Day, R.W. & Quinn, G.P. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs*, **59**, 443-463.

- Day, T.A. & Detling, J.K. (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology*, **71**, 180-188.
- Esselink, P., Helder, G.J.F., Aerts, B.A. & Gerdes, K. (1997) The impact of grubbing by Greylag Geese (*Anser anser*) on the vegetation dynamics of a tidal marsh. *Aquatic Botany*, **55**, 261-279.
- Frank, D.A. & Groffman, P.M. (1998) Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology*, **79**, 2229-2241.
- Frank, D.A. & McNaughton, S.J. (1992) The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology*, **73**, 2043-2058.
- Ganter, B., Cooke, F. & Mineau, P. (1996) Long-term vegetation changes in a Snow Goose nesting habitat. *Canadian Journal of Zoology*, **74**, 965-969.
- Gauthier, G., Hughes, R.J., Reed, A., Beaulieu, J. & Rochefort, L. (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653-664.
- Giroux, J.-F. & Bédard, J. (1987) The effects of grazing by greater snow geese on the vegetation of tidal marshes in the St Lawrence estuary. *Journal of Applied Ecology*, **24**, 773-788.
- Gray, A.J. & Scott, R. (1980) A genecological study of *Puccinellia maritima* Huds. (Parl.). I. Variation estimated from single-plant samples from British populations. *New Phytologist*, **85**, 89-107.

- Haynes, R.J. (1986) The decomposition process: mineralization, immobilization, humus formation, and degradation. *Mineral Nitrogen in the Plant-Soil System* (ed. R.J. Haynes), pp. 52-126. Academic Press Inc., Orlando, Florida.
- Hik, D.S. & Jefferies, R.L. (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *Journal of Ecology*, **78**, 180-195.
- Hik, D.S., Sadul, H.A. & Jefferies, R.L. (1991) Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. *Journal of Ecology*, **79**, 715-730.
- Hultén, E. (1968) *Flora of Alaska and Neighboring Territories*. Stanford University Press, Stanford, California.
- Hupp, J.W., Robertson, D.G. & Schmutz, J.A. (2000) Recovery of tall cotton-grass following real and simulated feeding by snow geese. *Ecography*, **23**, 367-373.
- Hupp, J.W., White, R.G., Sedinger, J.S. & Robertson, D.G. (1996) Forage digestibility and intake by lesser snow geese: effects of dominance and resource heterogeneity. *Oecologia*, **108**, 232-240.
- Hupp, J.W., Zacheis, A.B., Anthony, R.M., Robertson, D.G., Erickson, W.P. & Palacios, K.C. (2001) Snow cover and snow goose distribution during spring migration. *Wildlife Biology*, **in press**.
- Hyder, D.N. (1972) Defoliation in relation to vegetative growth. *The Biology and Utilization of Grasses* (eds V.B. Youngner & C.M. McKell), pp. 304-317. Academic Press, New York, New York.

- Jano, A.P., Jefferies, R.L. & Rockwell, R.F. (1998) The detection of vegetational change by multitemporal analysis of LANDSAT data: the effects of goose foraging. *Journal of Ecology*, **86**, 93-99.
- Kaye, J.P. & Hart, S.C. (1997) Competition for nitrogen between plants and soil microorganisms. *Trends in Ecology and Evolution*, **12**, 139-143.
- Kerbes, R.H., Baranyuk, V.V. & Hines, J.E. (1999) Estimated size of the Western Canadian Arctic and Wrangel Island lesser snow goose populations on their breeding and wintering grounds. *Distribution, Survival, and Numbers of Lesser Snow Geese of the Western Canadian Arctic and Wrangel Island, Russia* (eds. R.H. Kerbes, K.M. Meeres & J.E. Hines), pp.25-38. Canadian Wildlife Service Occasional Paper 98, Ottawa, Ontario.
- Kuehl, R.O. (1994) *Statistical Principles of Research Design and Analysis*. Duxbury Press, Belmont, California.
- Kotanen, P. & Jefferies, R.L. (1987) The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. *Journal of Ecology*, **75**, 961-975.
- Kotanen, P.M. & Jefferies, R.L. (1989) Responses of arctic sedges to release from grazing: leaf demography of *Carex xflavicans*. *Canadian Journal of Botany*, **67**, 1408-1413.
- Madsen, J. & Mortensen, C.E. (1987) Habitat exploitation and interspecific competition of moulting geese in East Greenland. *Ibis*, **129**, 25-44.

- McNaughton, S.J., Zungia, G., McNaughton, M.M. & Banyikwa, F.F. (1997) Ecosystem catalysis: soil urease activity and grazing in the Serengeti ecosystem. *Oikos*, **80**, 467-469.
- Meyer, G.A. (1998) Mechanisms promoting recovery from defoliation in goldenrod (*Solidago altissima*). *Canadian Journal of Botany*, **76**, 450-459.
- Miller, D.L., Smeins, F.E. & Webb, J.W. (1996) Mid-Texas coastal marsh change (1939-1991) as influenced by lesser snow goose herbivory. *Journal of Coastal Research*, **12**, 462-476.
- Mulder, C.P.H. & Ruess, R.W. (1998) Effects of herbivory on arrowgrass: interactions between geese, neighboring plants, and abiotic factors. *Ecological Monographs*, **68**, 275-293.
- Neter, J., Wasserman, W. & Kutner, M.H. (1990) *Applied Linear Statistical Models*, 3rd edn. Irwin, Homewood, Illinois.
- Nowak, R.S. & Caldwell, M.M. (1984) A test of compensatory photosynthesis in the field: implications for herbivory tolerance. *Oecologia*, **61**, 311-318.
- Olson, B.E. & Richards, J.H. (1988) Tussock regrowth after grazing: intercalary meristem and axillary bud activity of tillers of *Agropyron desertorum*. *Oikos*, **51**, 374-382.
- Painter, E.L., Detling, J.K. & Steingraeber, D.A. (1993) Plant morphology and grazing history: Relationships between native grasses and herbivores. *Vegetatio*, **106**, 37-62.

- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. & Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, **74**, 467-480.
- Person, B.T., Babcock, C.A. & Ruess, R.W. (1998) Forage variation in brood-rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska. *Journal of Ecology*, **86**, 243-259.
- Peterson, R.K.D., Danielson, S.D. & Higley, L.G. (1992) Photosynthetic responses of alfalfa to actual and simulated alfalfa weevil (Coleoptera: Curculionidae) injury. *Environmental Entomology*, **21**, 501-507.
- Prins, H.H.Th., Ydenberg, R.C. & Drent, R.H. (1980) The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. *Acta Botanica Neerlandica*, **29**, 585-596.
- Reed, A. (1990) Population dynamics in a successful species: challenges in managing the increasing population of greater snow geese. *Transaction of the 19th IUGB Congress at Trondheim*, **9**, 136-142.
- Rosenthal, J.P. & Kotanen, P.M. (1994) Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution*, **9**, 145-148.
- Ruess, R.W. & McNaughton, S.J. (1987) Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos*, **49**, 101-110.

- Ruess, R.W., Uliassi, D.D., Mulder, C.P.H. & Person, B.T. (1997) Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: Implications for geese-ecosystem dynamics in western Alaska. *Écoscience*, **4**, 170-178.
- Smith, T.J. III & Odum, W.E. (1981) The effects of grazing by snow geese on coastal salt marshes. *Ecology*, **62**, 98-106.
- Thomas, R.J., Logan, K.A.B., Ironside, A.D. & Bolton, G.R. (1988) Transformations and fate of sheep urine-N applied to an upland U.K. pasture at different times during the growing season. *Plant and Soil*, **107**, 173-181.
- Thomas, R.J., Logan, K.A.B., Ironside, A.D. & Bolton, G.R. (1990) The effects of grazing with and without excretal returns on the accumulation of nitrogen by ryegrass in a continuously grazed upland sward. *Grass and Forage Science*, **45**, 65-75.
- Thomas, R.J., Logan, K.A.B., Ironside, A.D. & Milne, J.A. (1986) Fate of sheep urine-N applied to an upland grass sward. *Plant and Soil*, **91**, 425-427.
- von Ende, C.N. (1993) Repeated-measures analysis: growth and other time-dependent measures. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 113-137. Chapman & Hall, New York, New York.
- Wilkens, K.A. & Cooch, E.G. (1999) *Waterfowl Population Status, 1999*. U.S. Fish & Wildlife Service, Washington D.C.
- Wilson, D.J., van der Wal, R., Chang, E.R., Jensen, A. & Jefferies, R.L. (1999) Urea hydrolysis and nitrification in arctic salt-marsh soils: Possible constraints on the growth of forage plants. *Écoscience*, **6**, 72-78.

- Ydenberg, R.C. & Prins, H.H.Th. (1981) Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology*, **18**, 443-453.
- Zaady, E., Groffman, P.M. & Shachak, M. (1996) Release and consumption of nitrogen by snail feces in Negev Desert soils. *Biology and Fertility of Soils*, **23**, 399-404.
- Zacheis, A., Hupp, J.W. & Ruess, R.W. (2000) Effects of migratory geese on plant communities of an Alaskan salt marsh. *Journal of Ecology*, **in press**.
- Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, New Jersey.
- Zellmer, I.D., Clauss, M.J., Hik, D.S. & Jefferies, R.L. (1993) Growth responses of arctic graminoids following grazing by captive lesser snow geese. *Oecologia*, **93**, 487-492.

Table 3.1 *F*-values from repeated measures MANOVA analyses for vegetation characteristics, captive goose experiment, Susitna Flats, Alaska. *Carex ramenskii* and *Triglochin maritimum* biomass and shoot nitrogen concentration were sampled in July and August 1996; all other variables were sampled in August 1996 and 1997. All *F*-tests are single degree of freedom tests, with denominator degrees of freedom reported. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

	Contrasts				Time x Contrast Interactions			
					Time x	Time x	Time x	
	Grazed vs. Ungrazed	Long vs. Short	Faeces vs. No faeces	Time	(Grazed vs. Ungrazed)	(Long vs. Short)	(Faeces vs. No faeces)	df
<i>Carex ramenskii:</i>								
Biomass	0.19	3.02	0.24	5.52*	1.62	1.00	0.15	76
Tillers	6.88**	0.05	5.41*	20.58***	0.60	7.11**	0.74	76
Inflorescences	1.04	0.01	0.01	27.58***	0.89	0.08	3.05	76
N concentration	0.00	1.38	0.67	56.30***	6.87**	1.88	3.00	77
<i>Triglochin maritimum:</i>								
Biomass	0.00	0.64	1.51	1.53	5.66*	0.18	0.25	76
Tillers	0.95	0.01	0.46	1.53	3.80*	3.29	0.49	76
Inflorescences	6.22**	1.27	0.08	71.93***	1.10	0.03	0.06	76
N concentration	1.74	0.44	0.23	0.62	3.68*	0.01	3.67*	75
Standing dead	0.81	1.99	0.04	232.18***	8.31**	1.29	0.11	74
Litter	37.49***	1.29	7.42**	51.49***	17.88***	0.64	0.00	74

Table 3.2 *F*-values from repeated measures MANOVA analyses for soil characteristics, captive goose experiment, Susitna Flats, Alaska. Data were collected in May, July, and August 1996. * $P \leq 0.05$, *** $P \leq 0.001$

	Contrasts			Time	Time x Contrast Interactions		
	Grazed vs. Ungrazed	Long vs. Short	Faeces vs. No faeces		Time x (Grazed vs. Ungrazed)	Time x (Long vs. Short)	Time x (Faeces vs. No faeces)
Total soil C	0.51	0.33	0.00	0.18	0.25	1.33	0.54
Total soil N	0.28	1.01	0.19	34.41***	0.08	0.28	0.58
C mineralization	0.16	0.42	5.00*†	25.78***	1.08	0.22	0.84
N mineralization	0.09	0.32	0.42	14.13***	0.20	0.09	1.75
d.f.	1, 56	1, 56	1, 56	2, 55	2, 55	2, 55	2, 55

† significant on ranks only

Figure 3.1 Vegetation removed by geese (offtake) in captive goose experiment, May 1996, Susitna Flats, Alaska. Offtake in all grazed plots (long + short period plots), and in long and short period plots separately for (A) total offtake (*Carex ramenskii* + *Triglochin maritimum*), (B) *Carex ramenskii* offtake, and (C) *Triglochin maritimum* offtake.

Offtake significantly greater than zero is indicated by * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. Means \pm 1 S.E. are reported.

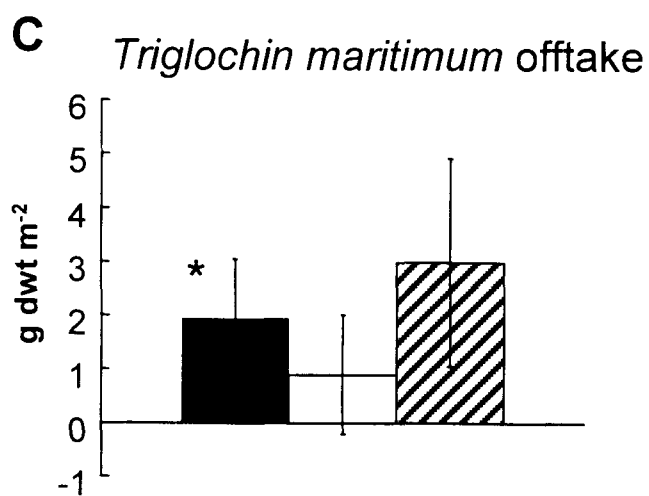
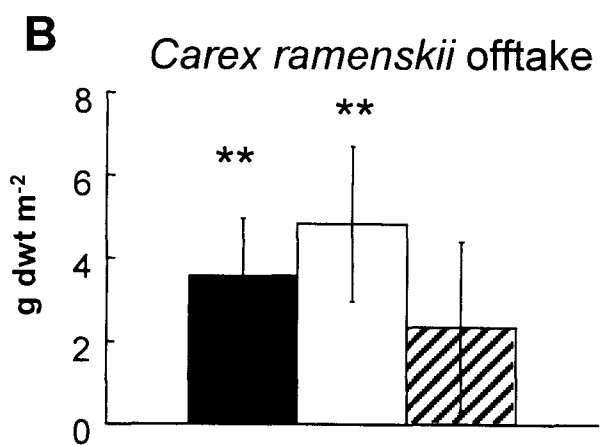
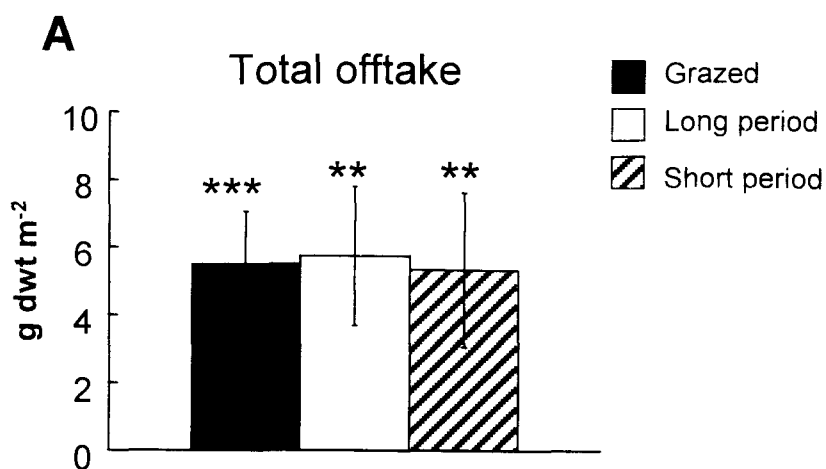
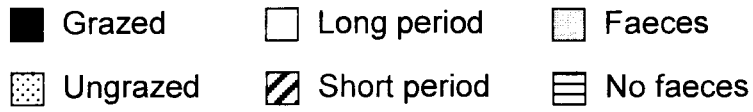
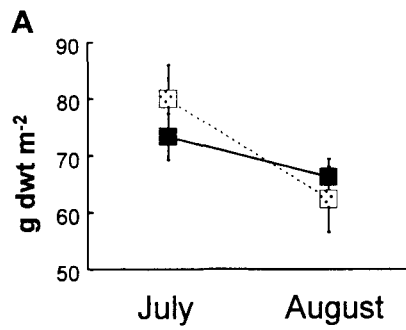


Figure 3.2 Biomass in treatment plots, captive goose experiment, July and August 1996, Susitna Flats, Alaska. Comparison of (A) all grazed plots (long + short period plots) and ungrazed controls, (B) long and short period plots, and (C) faeces and no faeces plots in for *Carex ramenskii* biomass and (D-F) *Triglochin maritimum* biomass. Significant differences between contrasts ($P \leq 0.01$) are based on separate monthly analyses and are indicated by **. Means \pm 1 S.E. are reported.



Carex ramenskii
biomass



Triglochin maritimum
biomass

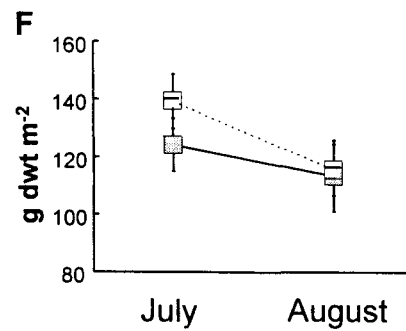
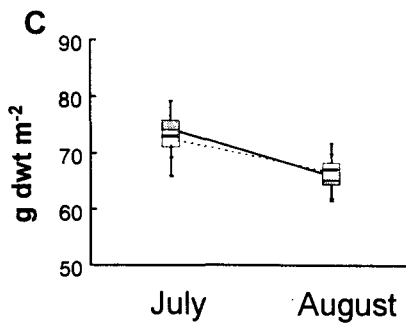
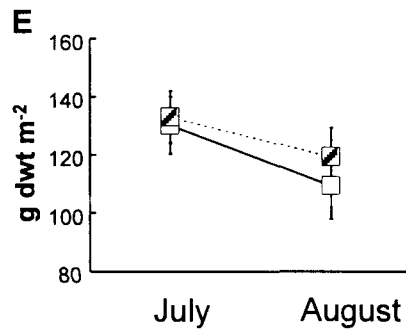
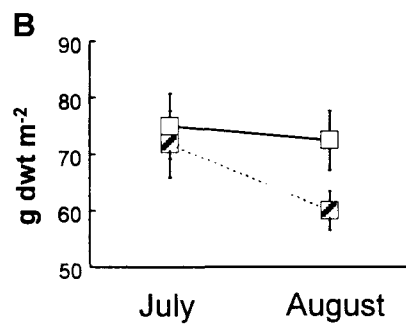
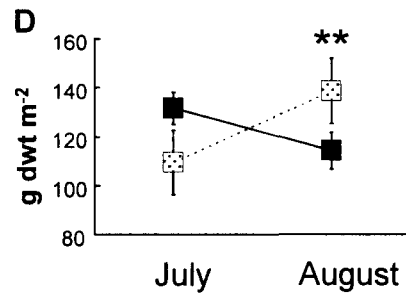


Figure 3.3 Tiller density in treatment plots, captive goose experiment, August 1996 and 1997, Susitna Flats, Alaska. Comparison of (A) all grazed plots (long + short period plots) and ungrazed controls, (B) long and short period plots, and (C) faeces and no faeces plots for *Carex ramenskii* tiller density and (D-F) *Triglochin maritimum* tiller density. Significant differences between contrasts ($P \leq 0.05$) are based on separate monthly analyses and are indicated by *. Means ± 1 S.E are reported.

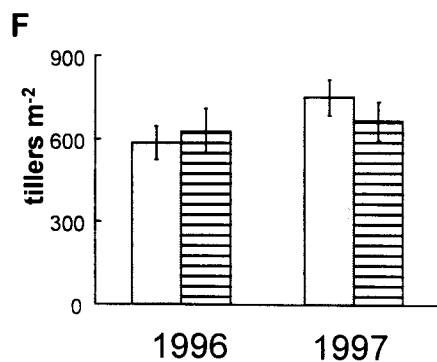
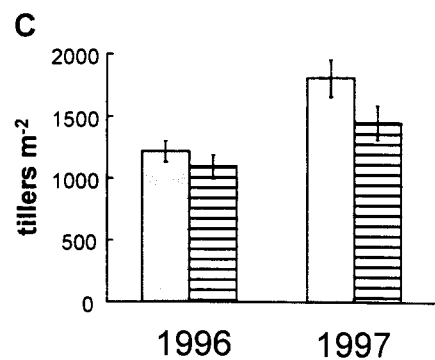
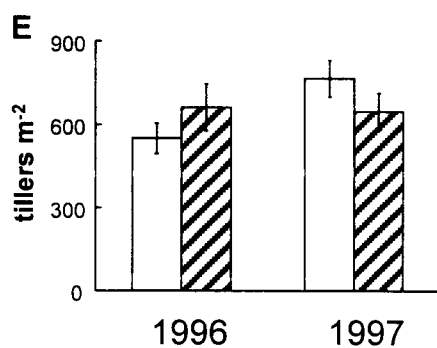
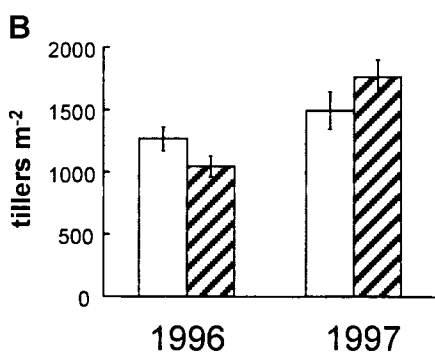
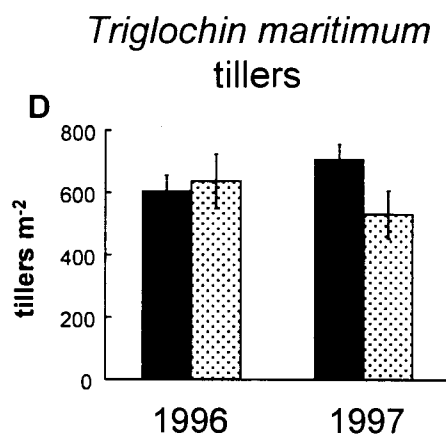
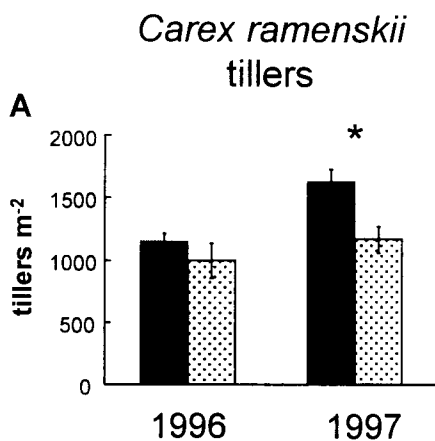
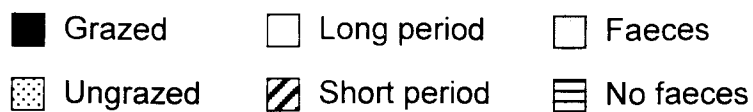
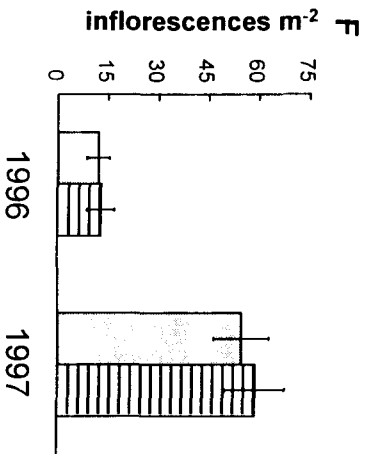
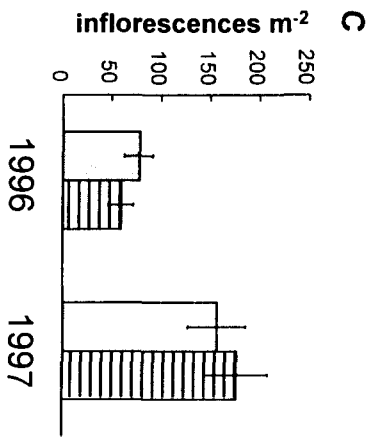
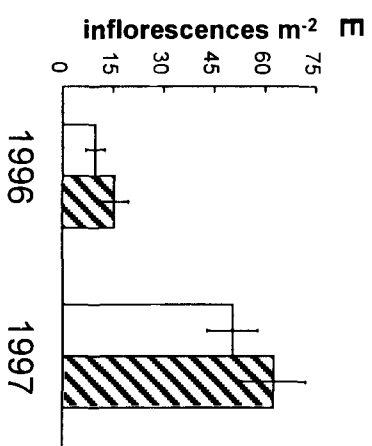
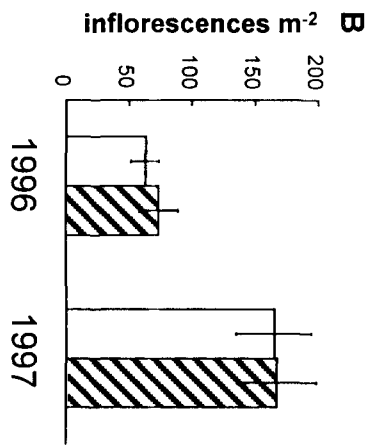
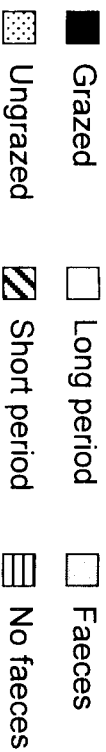


Figure 3.4 Inflorescence density in treatment plots, captive goose experiment, August 1996 and 1997, Susitna Flats, Alaska. Comparison of (A) all grazed plots (long + short period) and ungrazed controls, (B) long and short period plots, and (C) faeces and no faeces plots for *Carex ramenskii* inflorescence density and (D-F) *Triglochin maritimum* inflorescence density. Significant differences between contrasts ($P \leq 0.05$) are based on separate monthly analyses and are indicated by *. Means ± 1 S.E. are reported.





Carex ramenskii
inflorescences

Triglochin maritimum
inflorescences

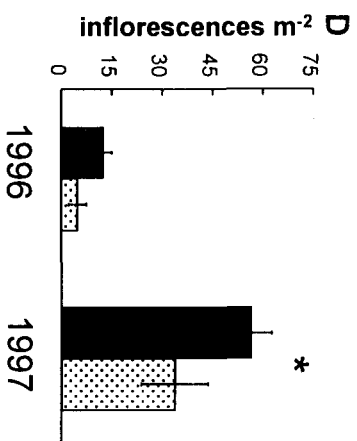
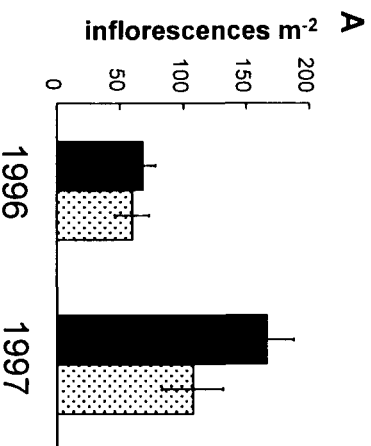


Figure 3.5 Nitrogen concentrations in vegetation in treatment plots, captive goose experiment, July and August 1996, Susitna Flats, Alaska. Comparison of (A) all grazed plots (long + short period plots) and ungrazed controls, (B) long and short period plots, and (C) faeces and no faeces plots for *Carex ramenskii* and (D-F) *Triglochin maritimum*. Means \pm 1 S.E. are reported. There were no significant differences between contrasts.

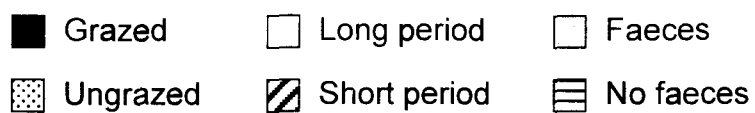
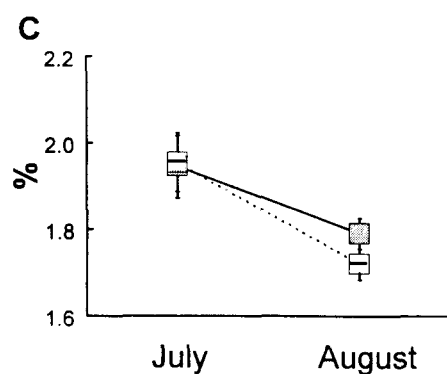
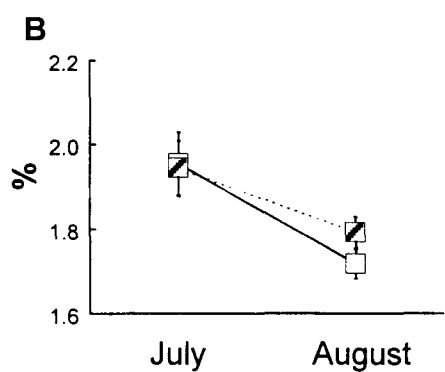
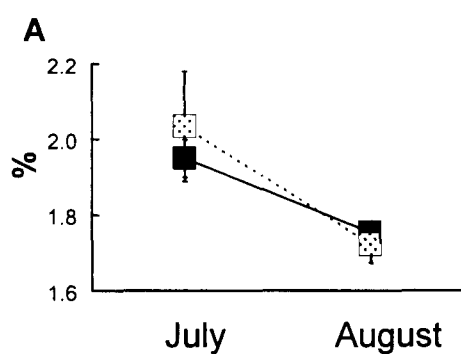
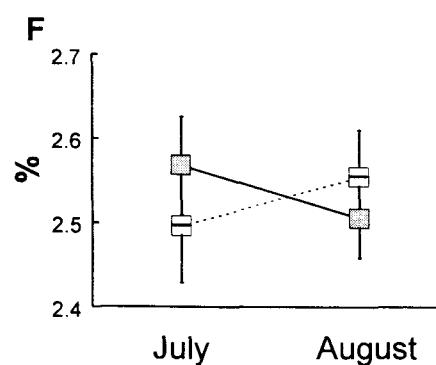
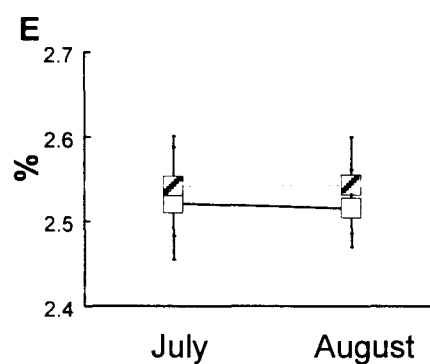
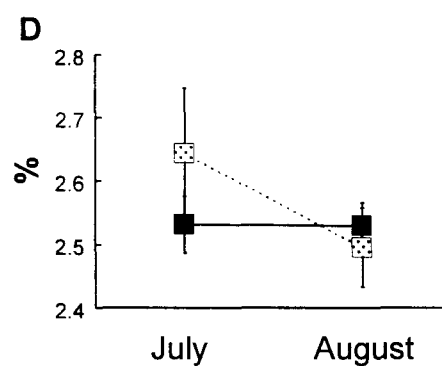
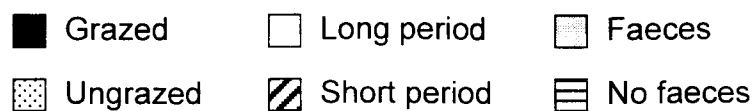
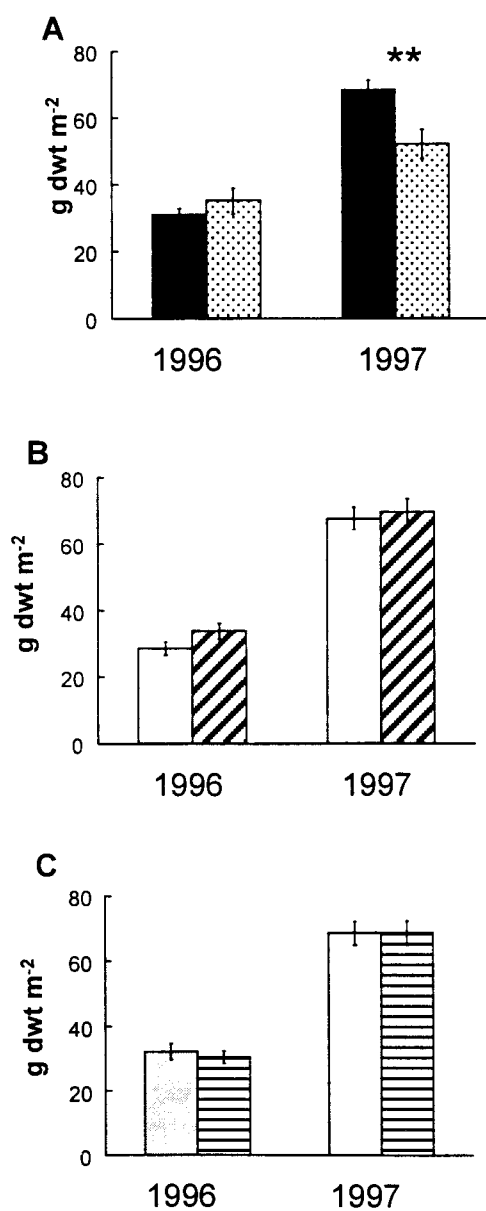
*Carex ramenskii**Triglochin maritimum*

Figure 3.6 Standing dead and litter biomass in treatment plots, captive goose experiment, August 1996 and 1997, Susitna Flats, Alaska. Comparison of (A) all grazed plots (long + short period plots) and ungrazed controls, (B) long and short period plots, and (C) faeces and no faeces plots for standing dead biomass and (D-F) litter biomass. Significant differences between contrasts are based on separate monthly analyses and are indicated by ** $P \leq 0.01$, *** $P \leq 0.001$. Means ± 1 S.E. are reported.



Standing Dead Biomass



Litter Biomass

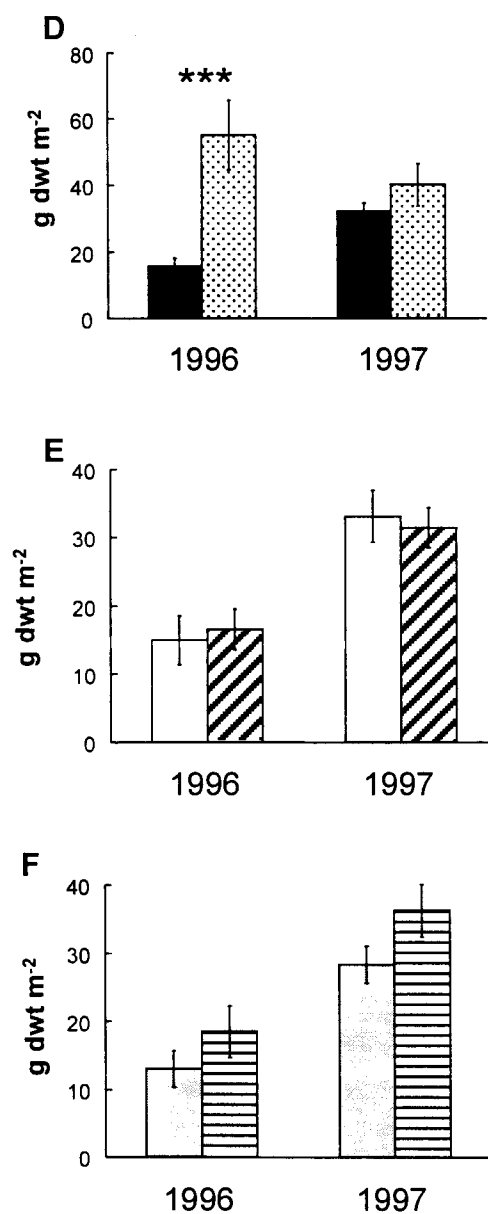
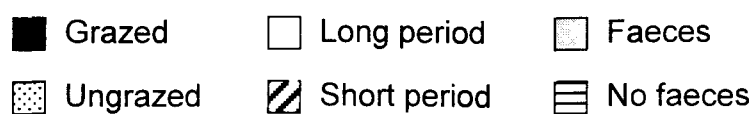
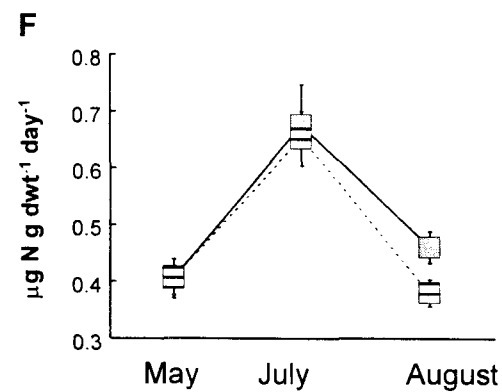
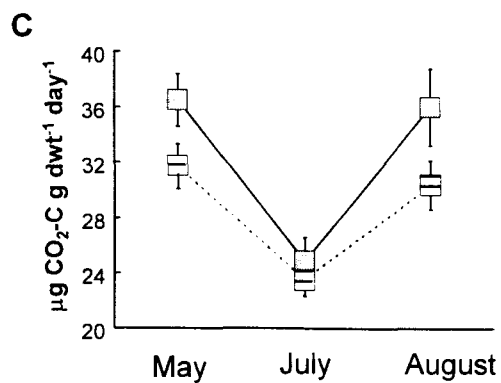
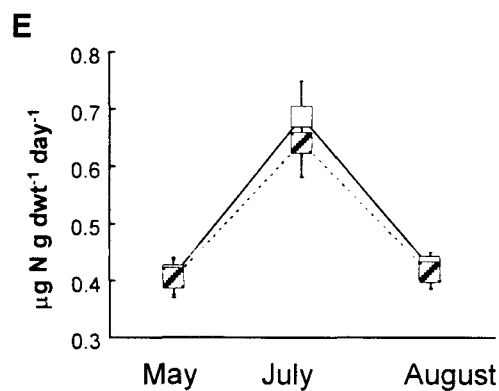
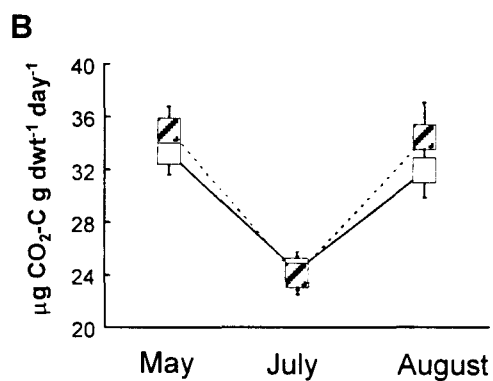
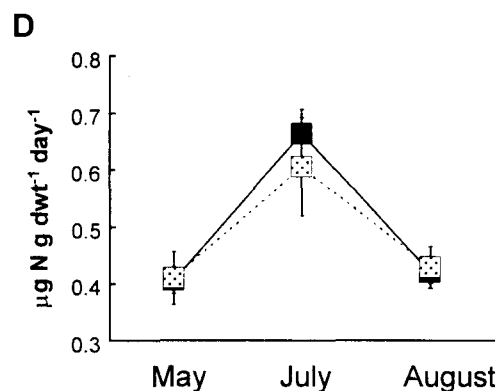
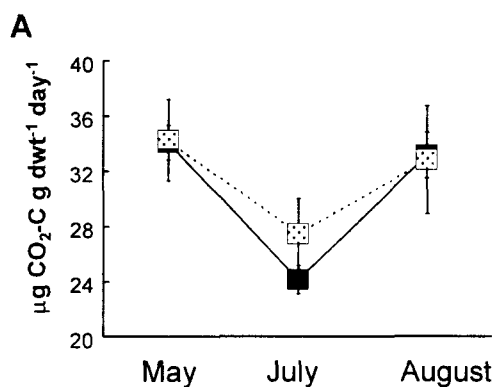


Figure 3.7 Soil carbon and nitrogen mineralization on treatment plots, captive goose experiment, May to August 1996, Susitna Flats, Alaska. Comparisons of (A) all grazed plots (long + short period plots) and ungrazed controls, (B) long and short period plots, and (C) faeces and no faeces plots for carbon mineralization and (D-F) nitrogen mineralization. Means \pm 1 S.E. are reported. There were no significant differences between contrasts based on separate monthly analyses.



Carbon Mineralization

Nitrogen Mineralization



CONCLUSIONS

The effects of geese on plant communities in Susitna Flats were dependent upon the type of herbivory (i.e., above- or below-ground), the growth form of plant species, and competitive interactions with plant neighbors. These variables, and the effects of herbivory, differed between the herb meadow and the sedge meadow communities. In the sedge meadow community, where feeding was primarily on aboveground shoots, herbivory had no effect on the biomass of the dominant species *Carex ramenskii* and *Triglochin maritimum*. These species have characteristics conferring tolerance to herbivory, such as belowground carbohydrate reserves, protected basal meristems located at or below soil surfaces, and carbohydrate production in undamaged tillers or shoots (Hyder 1972; Youngner 1972; Archer & Tieszen 1986; Rosenthal & Kotanen 1994; Crawley 1997). Geese fed on plants at an early phenological stage, and *T. maritimum* and *C. ramenskii* were able to fully compensate for tissue loss by the end of the growing season. In fact, the sedge meadow community showed no effects of herbivory on plant biomass at foraging intensity 10 times that imposed by wild geese, as evidenced by an experiment using captive geese, indicating that this community is highly resilient to goose herbivory.

In contrast, geese grubbed for belowground plant tissues in the herb meadow community, a type of feeding more likely to cause plant mortality. *Plantago maritima* roots, which are easily extracted from soil, comprised 40% of snow goose diets. Grubbing reduced *P. maritima* biomass, and incidentally caused a substantial decrease in *Potentilla egedii* biomass in grazed areas. In the spring, *P. egedii* exists as a small corm

located near the soil surface with few roots. Although geese did not feed on *P. egedii*, grubbing by geese for other plant species may damage it, and with little storage capacity or aboveground growth, *P. egedii* may have difficulty recovering from damage. In contrast, snow geese fed on *T. maritimum* root crowns, but did not affect biomass of this species. *T. maritimum* taproots are firmly rooted and difficult for geese to remove, so that belowground feeding probably had little effect on plant mortality. *C. ramenskii* had more biomass in grazed plots compared to exclosed in the herb meadow. Greater growth of *C. ramenskii* in grazed areas was likely due to reduced competition from *P. maritima* and *P. egedii*, as well as to tolerance of herbivory (Ruess *et al.* 1997).

The results from the two plant communities suggest that the type of herbivory (i.e., above- or belowground) interacts with plant morphology (e.g., meristem location, how firmly plants are rooted to soil) to determine plant tolerance to herbivory. In addition, the effect of herbivory on a particular plant species may depend on the community in which it is found (i.e., *C. ramenskii* had greater biomass in grazed plots in the herb meadow but there were no differences between grazed and exclosed plots in the sedge meadow community). Therefore, the response of an individual species to herbivory is partly dependent on who its neighbors are.

Effects of geese on nitrogen dynamics also differed between communities, mainly because soils were much drier in the herb meadow community. Geese increased mineralization rates in the sedge meadow by trampling litter into wet soils in the spring. Litter incorporated into soils increased organic nitrogen pool size and decreased soil C:N ratios, which resulted in greater rates of nitrogen mineralization. Trampling also

increased the extent of bare, non-littered soil in the marsh, which facilitated the growth of nitrogen-fixing cyanobacteria. Nitrogen from cyanobacterial mats increased organic nitrogen pool size and again led to higher mineralization rates in trampled areas. In contrast, early snow melt in 1997 in the herb meadow left soils dry, so that trampling could not as easily incorporate litter into soils.

Due to unique characteristics of the sedge meadow community, trampling could be identified as the mechanism through which herbivores increased nitrogen availability, as opposed to other established mechanisms (alterations in litter quality, litter biomass, root biomass, or microclimate by herbivores, or through fecal input; Holland & Detling 1990; Pastor *et al.* 1993; Biondini *et al.* 1998; Frank & Groffman 1998; van Wijnen *et al.* 1999; Sirotnak & Huntly 2000). Soil moisture was very high, and vegetative cover very low, so that trampling by geese resulted in a nearly complete lack of litter on the soil surface after birds departed in the spring. Wetland soils had low organic matter content, so that litter inputs from trampling were not masked by nutrient contributions from a large pool of previously existing organic material. Because the duration of use of the marsh by geese was short and plants were grazed at an early stage of development, litter production was not affected by grazing. Litter C:N ratios and microclimate variables such as soil moisture, temperature, and salinity did not differ between grazed and exclosed plots. Finally, because duration of use by geese was short, fecal nitrogen inputs were very small. A path analysis indicated that feces had no effect on organic nitrogen pool size or nitrogen mineralization rates. In fact, results from a captive goose

experiment indicated that fecal nitrogen additions 10 times greater than those in areas grazed by wild birds still did not affect nitrogen availability for plants.

The effects of geese on forage quality and availability differed between plant communities in Susitna Flats. In the sedge meadow, geese did not affect availability of forage, as feeding did not alter plant biomass or relative species abundance. Although trampling increased nitrogen availability to plants in this community, the dominant species *C. ramenskii* and *T. maritimum* did not have higher shoot nitrogen concentrations in grazed areas. The lack of an effect of geese on both the quality and abundance of their forage plants has only been rarely documented (Zellmer *et al.* 1993). In Susitna Flats, the lack of a response to herbivory was because low plant biomass limited the duration for which geese were able to exploit sites, and because plant species were exploited at a very early stage of growth and were highly resilient to herbivory.

In the herb meadow community, geese reduced the availability of the forage plant *P. maritima* but increased the abundance of *C. ramenskii* in grazed areas. *C. ramenskii* may fill gaps in the snow goose diet left by the reduction of *P. maritima*, but it is not known how the overall quality of the diet will be affected, as these species differ in fiber content and nitrogen concentration. In this community, trampling did not affect nitrogen cycling; however, *P. maritima* and *P. egedii* had higher shoot nitrogen concentrations in grazed areas through an unknown mechanism. Higher nitrogen concentration in these species was not coincident with goose staging, but could potentially impact snow goose diet if higher nitrogen levels carry over into the next spring. Therefore, the relative

abundance of forage species in this community was altered by herbivory, but the specific effects on of herbivory on diet quality for geese are unknown.

LITERATURE CITED

- Archer, S.R. & Tieszen, L.L. (1986) Plant responses to defoliation: hierarchical considerations. *Grazing Research at Northern Latitudes* (ed. O. Gudmundson), pp. 45-59. Plenum Press, New York, New York.
- Bakker, C. & Loonen, M.J.J. (1998) The influence of goose grazing on the growth of *Poa arctica*: overestimation of overcompensation. *Oikos*, **82**, 459-466.
- Bazely, D.R. & Jefferies, R.L. (1985) Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. *Journal of Applied Ecology*, **22**, 693-703.
- Bazely, D.R. & Jefferies, R.L. (1986) Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *Journal of Ecology*, **74**, 693-706.
- Beaulieu, J., Gauthier, G. & Rochefort, L. (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology*, **84**, 905-914.
- Bélanger, L. & Bédard, J. (1994) Role of ice scouring and goose grubbing in marsh plant dynamics. *Journal of Ecology*, **82**, 437-445.
- Bélanger, L., Giroux, J.-F. & Bédard, J. (1990) Effects of goose grazing on the quality of *Scirpus americanus* rhizomes. *Canadian Journal of Zoology*, **68**, 1012-1014.
- Biondini, M.E., Patton, B.D. & Nyren, P.E. (1998) Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. *Ecological Applications*, **8**, 469-479.

- Cargill, S.M. & Jefferies, R.L. (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 669-686.
- Crawley, M.J. (1990) Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology*, **27**, 803-820.
- Crawley, M.J. (1997) Plant-herbivore dynamics. *Plant Ecology* (ed. M.J. Crawley), pp. 401-474. Blackwell Science, Oxford.
- Day, T.A. & Detling, J.K. (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology*, **71**, 180-188.
- Esselink, P., Helder, G.J.F., Aerts, B.A. & Gerdes, K. (1997) The impact of grubbing by Greylag Geese (*Anser anser*) on the vegetation dynamics of a tidal marsh. *Aquatic Botany*, **55**, 261-279.
- Frank, D.A., & Groffman, P.M. (1998) Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology*, **79**, 2229-2241.
- Frank, D.A., Inouye, R.S., Huntly, N., Minshall, G.W. & Anderson, J.E. (1994) The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. *Biogeochemistry*, **26**, 163-188.
- Gauthier, G., Hughes, R.J., Reed, A., Beaulieu, J. & Rochefort, L. (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653-664.
- Giroux, J.-F. & Bédard, J. (1987a) The effects of grazing by greater snow geese on the vegetation of tidal marshes in the St. Lawrence estuary. *Journal of Applied Ecology*, **24**, 773-788.

- Giroux, J.-F. & Bédard, J. (1987b) Effects of simulated feeding by snow geese on *Scirpus americanus* rhizomes. *Oecologia*, **74**, 137-143.
- Hik, D.S. & Jefferies, R.L. (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *Journal of Ecology*, **78**, 180-195.
- Hik, D.S., Sadul, H.A. & Jefferies, R.L. (1991) Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. *Journal of Ecology*, **79**, 715-730.
- Holland, E.A. & Detling, J.K. (1990) Plant response to herbivory and belowground nitrogen cycling. *Ecology*, **71**, 1040-1049.
- Hupp, J.W., Robertson, D.G. & Schmutz, J.A. (2000) Recovery of tall cotton-grass following real and simulated feeding by snow geese. *Ecography*, **23**, 367-373.
- Hyder, D.N. (1972) Defoliation in relation to vegetative growth. *The Biology and Utilization of Grasses* (eds. V.B. Youngner & C.M. McKell), pp. 304-317. Academic Press, New York, New York.
- Manley, J.T., Schuman, G.E., Reeder, J.D. & Hart, R.H. (1995) Rangeland soil carbon and nitrogen responses to grazing. *Journal of Soil and Water Conservation*, **50**, 294-298.
- McNaughton, S.J. (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist*, **113**, 691-703.

- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. & Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, **74**, 467-480.
- Person, B.T., Babcock, C.A. & Ruess, R.W. (1998) Forage variation in brood-rearing areas used by pacific black brant geese on the Yukon-Kuskokwim delta, Alaska. *Journal of Ecology*, **86**, 243-259.
- Prins, H.H.Th., Ydenberg, R.C. & Drent, R.H. (1980) The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. *Acta Botanica Neerlandica*, **29**, 585-596.
- Ritchie, M.E., Tilman, D. & Knops, J.M.H. (1998) Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology*, **79**, 165-177.
- Rosenthal, J.P. & Kotanen, P.M. (1994) Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution*, **9**, 145-148.
- Ruess, R.W. & McNaughton, S.J. (1987) Grazing and the dynamics of nutrient and energy related microbial processes in the Serengeti grasslands. *Oikos*, **49**, 101-110.
- Ruess, R.W., Uliassi, D.D., Mulder, C.P.H. & Person, B.T. (1997) Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: Implications for geese-ecosystem dynamics in western Alaska. *Écoscience*, **4**, 170-178.
- Sirotnak, J.M. & Huntly, N.J. (2000) Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology*, **81**, 78-87.

- Smith, T.J. III (1983) Alteration of salt marsh plant community composition by grazing snow geese. *Holarctic Ecology*, **6**, 204-210.
- Smith, T.J. III & Odum, W.E. (1981) The effects of grazing by snow geese on coastal salt marshes. *Ecology*, **62**, 98-106.
- Thomas, R.J., Logan, K.A.B., Ironside, A.D. & Bolton, G.R. (1988) Transformations and fate of sheep urine-N applied to an upland U.K. pasture at different times during the growing season. *Plant and Soil*, **107**, 173-181.
- Thomas, R.J., Logan, K.A.B., Ironside, A.D. & Bolton, G.R. (1990) The effects of grazing with and without excretal returns on the accumulation of nitrogen by ryegrass in a continuously grazed upland sward. *Grass and Forage Science*, **45**, 65-75.
- van Wijnen, H.J., van der Wal, R. & Bakker, J.P. (1999) The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. *Oecologia*, **118**, 225-231.
- Ydenberg, R.C. & Prins, H.H.Th. (1981) Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology*, **18**, 443-453.
- Youngner, V.B. (1972) Physiology of defoliation and regrowth. *The Biology and Utilization of Grasses* (eds. V.B. Youngner & C.M. McKell), pp. 292-303. Academic Press, New York, New York.
- Zaady, E., Groffman, P.M. & Shachak, M. (1996) Release and consumption of nitrogen by snail feces in Negev Desert soils. *Biology and Fertility of Soils*, **23**, 399-404.

Zellmer, I.D., Clauss, M.J., Hik, D.S. & Jefferies, R.L. (1993) Growth responses of arctic graminoids following grazing by captive lesser snow geese. *Oecologia*, **93**, 487-492.